Genetic analysis of resistance to stripe rust in durum wheat (*Triticum turgidum* L. var. durum)

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ABSTRACT

Stripe rust, caused by the fungal pathogen *Puccinia striiformis* f. sp. *tritici* (*Pst*), is an important disease of durum wheat (*Triticum turgidum* L. var. durum) worldwide. Epidemics of stripe rust can reduce wheat yield more than 70% if infection occurs at early growth stages. Although fungicides can effectively prevent disease development and yield loss, use of resistant cultivars is the best approach for managing stripe rust. Currently, there is a lack of information on the genetic basis of resistance to stripe rust in durum wheat. The objective of this research was to characterize adapted durum wheat germplasm for resistance to prevalent races of stripe rust in Western Canada, to evaluate the inheritance of resistance, and to identify DNA markers associated with stripe rust resistance to assist in breeding for disease resistance. Field and phytotron experiments were assessed on a core collection of 92 diverse cultivars and breeding lines collected from major durum wheat breeding programs globally. The 92 lines were genotyped using a 90,000 single-nucleotide polymorphism (SNP) iSelect assay, which generated 13,539 polymorphic markers to perform association mapping. After adjustment for population structure, a major QTL for stripe rust resistance was identified on the long arm of chromosome 7BL. In the second study, a mapping population consisting of 155 double haploid durum wheat lines from the cross Kofa (susceptible) x W9262-260D3 (moderately resistant) were evaluated for stripe rust resistance in field and greenhouse experiments. Mendelian analysis revealed the presence of at least two resistance genes. Subsequent quantitative trait locus (QTL) analysis was performed using a genetic map consisting of 4,251 polymorphic markers spanning all 14 durum wheat chromosomes. Two significant QTLs were identified on chromosome 5BL (*QYr.usw-5B*) and 7BL (*QYr.usw-7B*), and explained 10.7 and 30.4% of the phenotypic variance, respectively. Both *QYr.usw-5B* and *QYr.usw-7B* are complementary genes and act together to express resistance. The QTL located on chromosome 7BL, identified in the DH mapping population, was in the same genetic interval as that identified using association mapping. These insights into the genetic basis of stripe rust resistance can be applied to enhance all-stage and durable resistance to stripe rust in durum wheat.

Key words: *Puccinia striiformis* f. sp. *tritici*, *Triticum turgidum*, association mapping, stripe rust resistance, QTL analysis

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LIST OF ABBREVIATIONS

AFLP: Amplified fragment length polymorphism

AIC: Akaike-information criterion

AM: Association mapping

ANOVA: Analysis of variance

APR: Adult plant resistance

AUDPC: Area under the disease progress curve

CI: Confidence interval

CIM: Composite interval mapping

cM: CentiMorgan

CPS: Canada Prairie Spring Wheat

CPSR: Canada Prairie Spring Red

CPSW: Canada Prairie Spring White

CTAB: Cetyl trimethylammonium bromide

CWAD: Canadian Western Amber Durum

CWRS: Canadian Western Red Spring

DArT: Diversity array technology

DH: Double haploid

FDR: False discovery rate

FHB: Fusarium head blight

GG: Golden gate

GLM: General linear model

GS: Growth stage

GWAS: Genome-wide association studies

HTAP: high-temperature adult plant

IT: Infection type

LD: Linkage disequilibrium

LOD: Logarithm of odds

LS: Least square

LSD: Least significant difference

LSM: Least square mean

MAF: Minor allele frequency

MAS: Marker-assisted selection

MCMC: Markov chain Monte Carlo

MI: Mixed isolates

MLM: Mixed linear model

MR: Moderately resistant

MS: Moderately susceptible

MT: Million tons

MQTL: Meta-QTL

NGS: Next-generation sequencing

NIL: Near-isogenic lines

PCA: Principal component analysis

PIC: Polymorphism information content

Pst: *Puccinia striiformis* f. sp. *tritici*

QC: Quality control

Q-Q plot: Quantile-Quantile plot

QTL: Quantitative trait locus

RCBD: Randomized complete block design

RFLP: Restriction fragment length polymorphism

RIL: Recombinant inbred line

ROS: Reactive oxygen species

SNP: Single-nucleotide polymorphism

spi: Single pustule isolate

SSR: Simple sequence repeats

STS: Sequence-tagged site

1 Introduction

Durum wheat (*Triticum turgidum* L. var. durum, 2n = 4x = 28; AABB) is one of the most important food crops in regions with a relatively dry climate (CFIA, 2006). It has a comparative adaptive advantage over hexaploid wheat (*Triticum aestivum* L.) and other small grains under hot dry conditions. Worldwide, 21 countries produce durum wheat (Cakmak, et al., 2010) and the average area planted annually to durum wheat is approximately 18 million hectares annual production averages about 35 million tonnes (MT) (Gillen, 2013). The European Union (mainly Italy, Spain, and Greece) is the largest annual durum wheat producer (averaging 8 MT annually), while Canada is the second largest (4.6 MT) followed by Turkey (4 MT), the USA and Mexico (2.2 MT). The total annual durum production of North African countries is 4.6 MT (Gillen, 2013). In Canada, the province of Saskatchewan is the largest producer of durum wheat (84%) followed by Alberta (14%) and Manitoba (2%) (CFIA, 2006).

Stripe rust of wheat, also known as yellow rust, caused by the fungal pathogen *Puccinia striiformis* f. sp. *tritici* (*Pst*), is an important destructive disease of wheat worldwide. Stripe rust has a wide global distribution. In recent years, regional disease epidemics have occurred in the USA (particularly Pacific North-West), East Asia (north-west and south-west of China), South Asia (Nepal), Australasia (Australia) and East Africa (Kenya) (Wellings, 2010). In North America, stripe rust was first discovered in 1915 near Sacaton, Arizona, USA and has become one of the most important diseases of wheat in western North America since the 1960s (Line, 2002). In Canada, stripe rust was discovered near Edmonton, Alberta in 1918 and in Saskatchewan in 1928, but was not considered an economically important disease in Canada. However, since 2000, stripe rust has appeared more frequently in regions east of the Rocky Mountains (Chen, et al., 2010) and in 2010, and in 2011, there was a significant epidemic of stripe rust in southern Alberta and Saskatchewan.

Stripe rust can reduce grain yield of wheat significantly, and yield losses of 100% can occur under severe epidemics. Yield losses generally range up to 70% depending on cultivar, time of initial infection, and development rate and duration of the disease (Chen, 2005). In Canada, wheat cultivars are classified into classes of wheat,

depending largely on their end-uses. Usually, Canada Prairie Spring White (CPSW) wheat, many older cultivars of Canadian Prairie Spring Red (CPSR) wheat and Canadian Western Red Spring (CWRS) wheat are very susceptible to stripe rust (Randhawa, et al., 2012). Canadian Western Amber Durum (CWAD) wheat is generally considered to be more resistant to stripe rust than hexaploid wheat in Western Canada (Randhawa, et al., 2012), but during the 2011 epidemic, some registered durum cultivars were susceptible in southern Alberta. To control stripe rust of wheat effectively, integrated management strategy including planting resistant cultivars, monitoring disease observation plot and weather, applying foliar fungicide and seed treatments and modifying crop management should be employed (Hovmøller and Henriksen, 2008; Line, 2002). As one of the most important strategies to control stripe rust, planting resistant cultivars is economical/environmentally friendly and can minimize yield loss effectively (Peng, et al., 1999; Hu, et al., 2008).

Genetic resistance to stripe rust is available, and several studies have been conducted to study the inheritance of resistance in hexaploid wheat, and to identify DNA markers to effectively select for resistance in wheat breeding programs (William, et al., 2003; Lin and Chen, 2007; Santra, et al., 2008; Herrera-Foessel, et al., 2011; Ren, et al., 2012). However, due to the rapidly evolving pathogen population, only a few all-stage resistance genes (e.g., *Yr5* and *Yr15*) are still effective in wheat breeding programs (Chen, et al., 2010). Adult plant resistance (APR) genes have been identified, but the relative effectiveness can be influenced by several factors, such as genetic background of resistance genes, the number of APR genes present and the pathotypes of stripe rust present (Singh and Saari, 1992). In addition, some APR genes are more effective at higher temperatures and most begin to express as early as the stem elongation stage, Resistance due to APR genes alone may not be sufficient to prevent disease when the weather is cool and disease pressure is high at early growth stages of the crop. It is thus urgent to identify additional sources of resistance and to diversify the genes used in breeding programs to improve the level and durability of resistance in wheat cultivars. Compared to hexaploid wheat, very little is known of the genetic basis of stripe rust resistance in durum wheat. The goal of this research was to characterize the availability of stripe rust resistance in adapted durum wheat cultivars and breeding lines and to genetically localize resistance using

association mapping (AM) and QTL mapping strategies.

2 Literature review

2.1 Distribution of stripe rust in North America

Puccinia striiformis f. sp. *tritici* (*Pst*) is adapted to cool (7-20°C) environmental conditions (Singh and Saari, 1992; Fetch, et al., 2011) and generally disease occurs in temperate regions or higher altitudes in tropical regions (Chen, 2005). Based on geographic barriers, prevailing winds, crop cycles, rust occurrence, and virulence of *Pst* (Chen, 2005), Line and Qayoum (1992) and Line (2002) described seven epidemic regions in the United States and Canada (Figure 1). The stripe rust in Region 5 (northwestern Washington and southwestern British Columbia) and Region 1 (eastern Washington, northeastern Oregon, northern Idaho and southeastern British Columbia and southwestern Alberta) developed locally, because of both the suitable environmental conditions and the year-round cropping including spring and winter wheat, barley and grasses. In British Columbia and southeastern Alberta, there are mild winters, followed by cool spring and summer conditions. In these regions, production of winter and spring wheat overlap in a cropping system, which provides a green bridge for *Pst* to survive and develop. Region 2 (Montana and southeastern Alberta) is largely infected from Region 1, so epidemics occur when there is a severe epidemic in Region 1 the previous year (Chen, 2005). Saskatchewan belongs to Region 7, where inoculum comes from either British Columbia and Alberta or the Pacific Northwest or the Great Plains of the United States (Chen, 2005). Stripe rust in this region is infrequent on spring-planted wheat, but disease can develop in the summer (Line, 2002). There is increasing evidence that spores of *Pst* can overwinter in southeastern Alberta (Region 2), which can then infect spring wheat in the early spring.

Figure 1. Seven epidemic regions of stripe rust in USA and Canada (Line and Qayoum, 1992; Line, 2002). Region 1, eastern Washington, northeastern Oregon, northern Idaho, southeastern British Columbia and southwestern Alberta; Region 2, western Montana and southeastern Alberta; Region 3, southern Idaho, southeastern Oregon, northern Nevada, northern Utah, and western Wyoming; Region 4, western Oregon and northern California; Region 5, northwestern Washington and southwestern British Columbia; Region 6, central and southern California and western Arizona; Region 7, the area east of the Rocky Mountains and southern Saskatchewan, Manitoba, and Ontario.

2.2 Stripe rust life cycle and host-pathogen interaction

The life cycle of Pst consists of continual uredinial generations (asexual cycle) and possible a sexual cycle using barberry plants (*Berberis* spp.) as alternate host. For the asexual disease cycle, urediniospores are responsible for annual recurrence, repeating and overwintering stages. Urediniospores germinate after contact with free water at temperatures of 9 to 13°C (Singh and Saari, 1992). They can over-summer on wheat in regions with cool temperatures in summer and can spread over long distances (2000 km) to infect wheat. In the late summer, the urediniospores are blown to autumn-sown wheat. In the winter, the urediniospores can survive in living leaf tissues above -4°C temperatures, or live under snow cover in regions where temperature is below -4°C (as low as -10°C). The urediniospores have a latent period in the winter up to 118 days. Sporulation and infection can occur when daytime temperatures reach 5°C (Singh and Saari, 1992; Carver, 2009). In Canada and the US, barberry plant, as alternate host of rust, shrub around the farmland was actively

eradicated in the 1910s, the further import, domestic movement, sale and propagation of barberry plants is under regulation, only black stem rust resistant cultivars of barberries is permitted to be sold commercially with restrictions (CFIA, 2012; Harmon, 2006). Therefore, sexual recombination of stripe rust is likely absence in North America, the variability in virulence is generated by introduction of exotic isolates, mutation and somatic hybridization (Park and Wellings, 2012; Jin, et al., 2010).

The sexual stage of the life cycle of *Pst* occurs after teliospores are produced in telial sori, on wheat, which can germinate immediately to produce basidiospores, but these are not involved in overwintering (Wright and Lennard, 1980). Basidiospores are capable of infecting the leaves of barberry plants, then pycnia and aecia are produced on barberry after infection, and the resultant aeciospores are able to inoculate wheat. Previous studies indicated that in areas where wheat and susceptible barberry species coexist, the variability in virulence is likely generated by sexual recombination. One of the indirect evidence was in western China, the Caucasus, Central Asia and eastern Africa, where susceptible barberry species grew naturally, a high degree of virulence variation was found (Jin, et al., 2010).

Puccinia striiformis f. sp. *tritici* is an obligate biotrophic pathogen, which requires living tissue to survive and reproduce. The pathogen derives nutrients from the infection site of living wheat cells (Murray and Wales, 2005; Garnica, et al., 2013). Wheat responds to *Pst* infection through various defense compounds induced by the pathogen. With race specific resistance, plants with resistance (R) genes can recognize avirulence gene products from the pathogen, and the recognition triggers signal transduction cascades within the plant, including calcium and iron fluxes, and increases reactive oxygen species (ROS). The alteration of ion components in the cell and the breakdown of cellular components due to the presence of ROS cause hypersensitive cell death (hypersensitive response) (Wang, et al., 2009; Yu, et al., 2010). Host cell death adjacent to an infection site (chlorosis or necrosis) usually restricts pathogen expansion through wheat mesophyll cells. The pathogen eventually dies from the lack of nutrition (Yu, et al., 2010).

2.3 Physiological race surveys

Isolates of *Pst* are classified into races based on differential virulence patterns on wheat lines (cultivars or genotypes) that each contains a single or multiple R genes. These collections of lines are generally referred to as "differential sets". The differentials were first demonstrated in 1930 and Gassner and Straib (1932) established a differential system based on ten differential varieties, this system was further modified because some original races were indistinguishable based on this system. A hierarchical system was established where "world differentials" was used to differentiate broad characteristics of virulence all over the world, and regional subsidiary sets (e.g., Europe and North America) were used to characterize virulence with a region. The primary world differentials included 7 lines around 1970: 'Chinese 166', 'Lee', 'Heines Kolben', 'Vilmorin 23', 'Moro', 'Strubes Dickkopf', and Suwon 92 /Omar; 'Clement' and *Triticum spelta* var. album were added into world differentials in 1976 and 1990 (Chen, 2005). This system is still used in Europe and some other countries. In the USA, over the last three decades, the number of wheat genotypes used for differentiating isolates of *Pst* has grown to 20 (Table 1) (Chen, 2005). In China, the current Chinese differential set consists of 17 wheat genotypes. Analysis of virulence of *Pst* in Western Canada from 1984 to 2002 used the 17 World and European differentials series for 7 supplementary lines, which comprised cultivars of soft white spring wheat of local interest and cultivars containing different *Yr* genes from those of the World and European differentials (Su, et al., 2003). Afterwards, Wellings et al. (2004) developed near-isogenic lines (NILs) in the Avocet-*YrA* background, for the 20 *Yr* genes including *YrA*, *Yr1*, *Yr2*, *Yr5*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr15*, *Yr17*, *Yr18*, *Yr24*, *Yr26*, *Yr27*, *YrSP*, *Yr28*, *Yr29*, *Yr31* and *Yr32*, which are now considered as the universal set of differential lines used to classify stripe rust races and differentiating rust resistance genes (NILs are not listed in Table 1).

Table 1. Wheat genotypes used to differentiate races of *Pst* in Europe, USA, China and Canada (Cultivars used by more than one regions are indicated by a common color) (Su, et al. 2003; Zhan, et al. 2012).

World and European		**U.S.A.**		**China**		**Canada**	
Diff. Sets	*Yr* gene	Diff. Sets	*Yr* gene	Diff. Sets	*Yr* gene	Diff. Sets	*Yr* gene
Hybrid 46	*Yr3b, Yr4b*	Paha	*YrPa1,YrPa2,YrPa3*	Hybrid 46	*YrH46, Yr4b*	Hybrid 46	*Yr3b, Yr4b*
Chinese 166	*Yr1*	Lemhi	*Yr21*	Fulhard	Unknown	Lemhi	*Yr21*
Heines VII	*Yr2, Yr25, YrHVII*	Chinese 166	*Yr1*	Lutescens 128	Unknown	Chinese 166	*Yr1*
Moro	*Yr10, YrMor*	Heines VII	*Yr2,YrHVII*	Mentana	Unknown	Heines VII	*Yr2, Yr25, YrHVII*
Lee	*Yr7, Yr22, Yr23*	Moro	*Yr10,YrMor*	Virgilio	*YrVir1, YrVir2*	Moro	*Yr10, YrMor*
Clement	*Yr9, YrCle*	Lee	*Yr7,Yr22,Yr23*	Abbondanza	Unknown	Lee	*Yr7, Yr22, Yr23*
Compair	*Yr8, Yr19*	Fielder	*Yr6,Yr20*	Early premium	Unknown	Fielder	*Yr6, Yr20*
Triticum spelta var. album	*Yr5*	Clement	*Yr9,YrCle*	Funo	*YrA, +*	Clement	*Yr9, YrCle*
Spalding Prolific	*YrSP*	Compair	*Yr8,Yr19*	Danish 1	*Yr3*	Compair	*Yr8, Yr19*
Carstens V	*YrCV*	Druchamp	*Yr3a,YrD,YrDru*	Jubilejina II	*YrJu1, YrJu2, YrJu3, YrJu4*	*Triticum spelta* var. album	*Yr5*
Nord Desprez	*Yr3a, Yr4a, YrND*	AvSYr5NIL	*Yr5*	Fengchan 3	*Yr1*	*T. dicoccoides* selection G-25	*Yr15*
Suwon 92 /Omar	*YrSU*	Produra	*YrPr1,YrPr2*	Lovrin 13	*Yr9, +*	Spalding Prolific	*YrSP*
Vilmorin 23	*Yr3, Yr4a, YrV23*	Yamhill	*Yr2,Yr4a,YrYam*	Kangyin 655	*Yr1, YrKy1, YrKy2*	Carstens V	*YrCV*
Heines Peko	*Yr2, Yr6, Yr26*	Stephens	*Yr3a,YrS,YrSte*	Suwon 11	*YrSu*	Nord Desprez	*Yr3a, Yr4a, YrND*
Heines Kolben	*Yr2, Yr6*	Tyee	*YrTye*	Zhong 4	Unknown	Suwon 92 /Omar	*YrSU*
Reichersberg 42	*Yr7, Yr25*	Tres	*YrTr1,YrTr2*	Lovrin 10	*Yr9*	Owens	Unknown
Strubes Dickkopf	*YrSD*	Hyak	*Yr17, YrTye*	Trigo eureka	*Yr6*	Vilmorin 23	*Yr3, Yr4a, YrV23*
		Express	*YrExp1, YrExp2*			Heines Peko	*Yr2, Yr6, Yr26*
		AvSYr8NIL	*Yr8*			Heines Kolben	*Yr2, Yr6*
		AvSYr9NIL	*Yr9*			Reichersberg 42	*Yr7, Yr25*
						Opal	*Yr4b*
						Minister	*Yr3c, YrMin*
						Strubes Dickkopf	*YrSD*
						Capelle Desprez	*Yr3a, Yr4a, Yr16*

There were no published durum wheat differentials, but durum wheat cultivars used as differentials to identify leaf rust isolates are under construction (Goyeau, et al., 2012). Some durum wheat cultivars have been included as part of a differential set for stem rust (Gerechter-Amitai, et al., 1971).

2.4 Genetics of stripe rust resistance

Genetic resistance to stripe rust can be classified into six groups based on three criteria: growth stage, race-specificity and temperature sensitivity (Table 2) (Chen, 2013). Resistance is generally classified as race-specific and non-race specific resistance. Race-specific resistance is effective against specific races, while non-race specific resistance is effective against multiple races. There is also temperature non-sensitive resistance and temperature sensitive resistance. Temperature sensitive resistance is usually expressed at high temperature (night temperatures are above 10 °C, and daytime temperatures are above 20 °C) but are generally less effective at low temperatures (Chen, 2013).

Table 2. Types of stripe rust resistance based on growth stage, race-specificity and temperature sensitivity.

Criteria		**Seedling resistance**		**High-temperature adult-plant resistance (HTAP)**	**Adult plant resistance (AP)**		
Growth stage	All stage resistance	*	*				
	Adult plant resistance			*	*	*	*
Race-specificity	Race-specific resistance	*	*		*	*	
	Non-race-specific resistance			*			*
Temperature sensitivity	Non-temperature sensitive resistance	*				*	*
	High temperature resistance		*	*	*		

Seedling resistance, also known as race-specific all-stage resistance, is expressed throughout the life of the wheat plant and is highly effective in the presence of avirulent races (Wellings, et al., 2007). It is usually controlled by a single resistance gene. However due to rapid evolution of races, single gene resistance can breakdown rapidly (Cao, et al., 2012). In contrast, APR, also called non-hypersensitive, slow-

rusting or partial (quantitative) resistance, develops as the wheat plant matures. Depending on cultivar and growing conditions, expression begins during stem elongation to early head emergence, with maximum expression occurring during the boot stage (Singh and Saari, 1992).

Generally, APR is preferred for breeding because these genes have longer durability of resistance, and are not easily overcome by the pathogen (Chen, 2013). Slow-rusting is a general feature of APR genes, and is characterized by which shows compatible infection types, but reduced latent periods and these features exert less selection pressure on pathogens (Burdon, et al., 2014). Second, it is more difficult for the pathogen to adapt by mutation to defense based on the additive effects of multiple minor genes that constitutes slow-rusting resistance. Third, the two cloned slow-rusting genes in wheat, namely *Lr34*/*Yr18* (encoding an ABC transporter) and *Yr36* (encoding a kinaseSTART protein), suggest a different mechanism of slow-rusting resistance from the NBS-LRR (nucleotide-binding site-leucine-rich repeat) based R-gene resistance (Cao, et al., 2012), which is easily recognized by the pathogen. However, APR generally does not provide immunity to the pathogen, and is most effective when combined with race-specific resistance (Chen, 2013) or in combination with multiple APR genes (Herrera-Foessel, et al., 2011).

Numerous studies have been conducted on the genetics of stripe rust resistance in wheat. There are at least 67 named resistance genes from *Yr1* to *Yr67* (Appendix 1) and many temporarily designated genes (www.ars.usda.gov and www.shigen.nig.ac.jp) have been identified from different germplasm collections (Huang, et al., 2011; Lowe, et al., 2011; Zargar, et al., 2011; Cao, et al., 2012). Several slow-rusting stripe rust resistance genes, which are pleiotropic with other rust and powdery mildew resistance genes, or closely linked to other rust resistance genes, have been discovered (Herrera-Foessel, et al., 2011). To date, there are only four well-characterized, slow rusting genes *Lr34*/*Yr18* (7DS), *Lr46*/*Yr29* (1BL), *Lr67*/*Yr46* (near the centromere of 4DL) and *Sr2*/*Yr30* (3BS) that are effective in the field (Singh, et al., 2005; Rosewarne, et al., 2012).

Broad-sense heritability of stripe rust resistance has been reported to range from 75% to 95%, while narrow-sense heritability has been estimated at 39% to 85% (Zhang, et al., 2001). Marker assisted selection (MAS) is an effective tool to select for

resistance genes (Suenaga, et al., 2003). However, most of the marker discovery and genetics of stripe rust resistance has focused on hexaploid wheat, with very little work in durum wheat (Appendix 1). Among 67 officially named *Yr* genes, only three: *Yr53*, *Yr64* and *Yr65*, were detected in durum wheat recently (Xu, et al., 2013; Cheng, et al., 2014). In fact, very little is known about strip rust resistance in durum wheat and therefore, a better understanding of stripe rust resistance is a high priority.

2.5 Association mapping and QTL mapping in plants

Association mapping, also known as linkage disequilibrium mapping, is a population-based survey approach that identifies marker-trait relationships based on linkage disequilibrium (LD) (Flint-Garcia, et al., 2003; Slatkin, 2008). It has been used extensively as an alternative to traditional QTL mapping to dissect human diseases, and is a useful tool in plant genetic studies (Flint-Garcia, et al., 2003; Slatkin, 2008).

Association mapping provides several advantages to QTL analysis in bi-parental mapping populations. First, the individuals under study do not require familial relationship. This allows for the exploitation of the cumulative historical recombination of all of the lines in the study and leads to an increase in mapping resolution (Jannink, et al., 2001; Buntjer, et al., 2005; Pozniak, et al., 2012). Second, AM is more time and cost efficient than traditional QTL mapping because construction of a segregating population is not necessary, association mapping can be performed on collections of diverse genotypes or within breeding materials. Further savings can be realized through use of historical phenotypic datasets to detect marker-trait associations (Podlich, et al., 2004; Crossa, et al., 2007; Sneller, et al., 2009; Pozniak, et al., 2012). Third, rather than only assaying allelic diversity that segregates between the parents in the bi-parental population, association mapping population increased coverage of allelic diversity (Myles, et al., 2009; Korte and Farlow, 2013). However, false positive associations because of population structure and/or multiple tests of markers, and false negatives because of low power to detect QTLs with minor genetic effect can be problems associated with AM if appropriate statistical adjustments are not considered.

Association mapping is based on LD, which is caused by the nonrandom

association of alleles at different loci (Flint-Garcia, et al., 2003). Through association mapping, the historical linkage disequilibrium that has been preserved between a marker and the associated allele for the trait of interest can be identified. Linkage disequilibrium in populations can be caused by several factors. Genetically linked loci will show strong LD, with LD declining with greater genetic distance (Stich, et al., 2005). Selection also influences LD in the populations, for example, selection acting on a monogenic trait generates LD between physically linked loci, while selection acting on polygenic traits generates LD between unlinked loci. The LD can also be generated by population structure, relatedness or genetic drift. This can result in spurious associations between a marker and a phenotype when a marker is identified that is not physically linked to the locus responsible for a trait (Kraakman, et al., 2004; Maccaferri, et al., 2005).

The extent of linkage disequilibrium in a population will determine the resolution of QTL using association-mapping approaches. Linkage disequilibrium is usually measured as the difference between the observed and the expected frequency of the haplotype (*D* or *D'*) or correlation between a pair of loci (*r* or frequently r^2) (Somers, et al., 2007; Zhao, et al., 2007). Since |D′| is biased according to sample size (Weiss and Clark, 2002; Ke, et al., 2004), the squared value of the correlation between markers (r^2) is favored for association mapping. The genome-wide LD decay of hexaploid wheat and durum extends approximately 2-3 cM ($r^2 < 0.2$) (Somers, et al., 2007). The extent of LD patterns in hexaploid wheat have been investigated widely, with LD decay extending from less than 0.5 cM ($r^2 < 0.1$) (Tommasini, et al., 2007) to 10 cM ($r^2 < 0.2$) (Chao, et al., 2007), Hao et al. (2012) reported that LD decay could be greater than 500 kb with $r^2 < 0.2$. The LD decay of durum extends from 2-3 cM ($r^2 < 0.2$) (Somers, et al., 2007) to 20 cM ($r^2 < 0.2$) (Maccaferri, et al., 2005). The extent of LD has large variation between self-pollinating and outcrossing species, the LD between markers in outcrossing plants usually decays faster than inbreeding plants e.g., LD declines rapidly within 1-5 kb in maize (*Zea mays* L.) diverse inbred lines, 1.1 kb in cultivated sunflower, 0.3 kb in wild grapevine (Zhao, et al., 2014). Due to the large genome size of hexaploid wheat (15,961 Mb) and tetraploid (11,660 Mb), a typical whole genome association study in hexaploid wheat and durum requires about 32,000 and 23,300 Single nucleotide polymorphism (SNP) markers, respectively, to cover the whole genome with adequate density. Fortunately, several high-density SNP

platforms are available in wheat and these have been suggested as a useful tool for AM (Akhunov, et al., 2009; Wang, et al., 2014).

Detailed knowledge of the genetic and phylogenetic relationships that defines population structure is a prerequisite to control spurious associations (Pritchard, et al., 2000). Population structure is the presence of allele frequency differences among subpopulations in the AM panel, due to unrandom mating between subpopulations. The unrandom mating is largely caused by physical separation, followed by genetic drift of alleles. The non-causing loci might be detected if they are more prevalent in the subpopulation with higher disease rate, it is referred as type I error. Type II error is usually involved in case-control association studies (Tian, et al., 2008). Several methods have been suggested to statistically adjust for population structure to reduce both type I and type II error rate of AM. Bayesian clustering (Pritchard, et al., 2000; Falush, et al., 2003; Falush, et al., 2007) and principal component analysis (PCA) are two approaches that are utilized commonly in AM to define population structure (Patterson, et al., 2006; Price, et al., 2006). The Bayesian clustering approach can be used to infer the number of sub-populations (K) and to assign individuals to sub-populations based on membership proportion in each sub-population (Q-matrix) (Hubisz, et al., 2009). The number of sub-populations is usually first determined based on an *a priori* estimate, often using a PCA, or genetic similarity analysis. Principle component analysis is effective to reduce high-dimensional genotype data to a small number of dimensions to make it possible to visualize similarity and variability among individuals in a two- or three-dimension plot (Hu, et al., 2005).

Controlling for population structure can also be implemented in AM studies by incorporating familiar kinship relationships among lines (Zhu, et al., 2008). Generally a kinship coefficient is estimated from molecular data, which indicates the probability that two homologous genes are identical by state. The kinship coefficient can be measured either by clearly provided pedigree information or estimation from genotypic data. The latter is preferred, as in most cases, it is not possible to verify an accurate and complete pedigree record. The unified mixed model method simultaneously accounts for population structure (Q) and familial kinship (K) in association analysis, and thus reduces both type I and type II errors (Loiselle, et al., 1995; Yu, et al., 2006; Zhu, et al., 2008).

The statistical power to detect associations is highly correlated with allele frequencies (Myles, et al., 2009). Those markers with minor allele frequencies less than a minimum critical threshold (usually 0.10), tend to result in the identification of false positives associations (Tabangin, et al., 2009). So that genome-wide association study (GWAS) is usually designed to detect common alleles, while next-generation sequencing (NGS) method is best suited for comprehensive identification of both common and rare variants (Marian & Belmont, 2011). Previous studies indicated that rare genotypes were more likely to cause spurious association (Lam, et al., 2007) in GWAS. Thus rare alleles are usually removed or pooled into a single genotypic class prior to evaluating marker trait associations (Pritchard and Rosenberg, 1999; Maccaferri, et al., 2005; Somers, et al., 2007).

There are two general AM strategies that have been used to associate DNA markers with phenotypic expression of traits: genome-wide and candidate-gene AM (Hirschhorn and Daly, 2005; Zhu, et al., 2008). Genome-wide association mapping, or genome scan, surveys genetic variation in the whole genome to find signs of association for various complex traits (Risch and Merikangas, 1996). Candidate-gene association mapping, assesses polymorphisms in selected candidate genes that have purported roles in controlling phenotypic variation for specific traits (Zhu, et al., 2008). However, candidate-gene studies rely on an understanding the biological function of casual genes, usually on the basis of biological hypotheses or the location of the candidate within a previously determined linkage region. When the fundamental physiological effects of a disease are unknown, the candidate-gene approach is inadequate to fully explain the genetic basis of the disease (Hirschhorn and Daly, 2005).

QTL mapping and association studies provide complementary methods to explore natural variation (Verslues, et al., 2014). When both are conducted, they compensate for each other's limitations (Korte and Farlow, 2013). In durum, QTL mapping was used to detect QTLs co-segregating with resistance to powdery mildew (Ouyang, et al., 2014), fusarium head blight (Buerstmayr, et al., 2013), stem rust (Haile, et al., 2012) and leaf rust (Gireesh, et al., 2014; Buerstmayr, et al., 2014; Singh, et al., 2013). Association mapping has also been applied to investigate phenological traits and kernel weight (Maccaferri, et al., 2006), kernel yellow pigment concentration

(Reimer, 2008), leaf rust resistance (Maccaferri, et al., 2010) and drought-adaptive traits (Maccaferri, et al., 2011).

2.6 Single-nucleotide polymorphism (SNP) application in plants

Previously, wheat genotyping relied on amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR), diversity array technology (DArT) and/or genome-specific sequence-tagged site (STS) markers. However, these markers rely on low to medium-throughput detection systems, thus hindering their application in genomic breeding (Akhunov, et al., 2009; Trebbi, et al., 2011).

Single nucleotide polymorphisms are a ubiquitous and the most abundant type of genetic variation among individuals of the same species. In wheat, Somers et al. (2003) detected one SNP every 540 base pair (bp) of EST sequence, while Ravel et al. (2006) detected one SNP per 334 bp of genomic sequence on average. In recent years, SNP markers have become the preferred choice for genotyping, as they are amendable to high-throughput automation despite having a lower level of polymorphism than other type of markers because SNPs are mostly bi-allelic polymorphisms (Mammadov, et al., 2012). Recently, SNP markers have been shown to be ideally suited to the construction of high-resolution genetic maps and to discover marker-trait associations in AM experiments of wheat (Akhunov, et al., 2009). Recently, a 90K Infinium iSelect assay has been developed for wheat, largely from next generation transcriptome sequencing experiments of diversity panels (Mammadov, et al., 2012; Oraguzie, et al., 2007; Wang, et al., 2014; Chao, et al., 2009; Trick, et al., 2012; Trebbi, et al., 2011; Zegeye, et al., 2014), and a high-density map created from these markers is now available for durum wheat (Maccaferri, et al., 2014). Genotypic data from the 90K iSelect assay has been used to construct high-density map of hexaploid wheat consisting of 40,267 markers with an average density of 1.46 markers/cM (Wang, et al., 2014). Several thousand SNPs available on the 90K iSelect chip were derived from durum wheat, and a high-density map consisting of >33,000 SNP markers was recently developed from 13 bi-parental mapping populations (Maccaferri, et al., 2014). All 14 durum wheat chromosomes were saturated with SNP markers, with an average density of 1.13 markers/cM. Given the high density of markers available, the 90K iSelect assay has been suggested as a useful tool for bi-

parental and association mapping in wheat (Wang, et al., 2014; Maccaferri, et al., 2014).

3 Project hypothesis and objectives

Limited information exists on the extent of genetic diversity for stripe rust resistance in durum wheat. The hypotheses for this project were that: i. genetic variation exists for stripe rust resistance in durum wheat, and ii. genomic regions controlling stripe rust resistance can be identified through AM and QTL mapping.

The objectives of this project was to enhance the understanding of strip rust resistance in elite durum wheat cultivars determine genetic control of stripe rust resistance in durum wheat and to identify molecular markers that can be applied in breeding programs to select for resistance. There are four specific activities related to accomplishing these objectives:

i. to characterize a durum wheat association-mapping panel for stripe rust resistance;

ii. to map stripe rust resistance loci and identify markers associated with resistance using AM and QTL mapping methods;

iii. to evaluate the inheritance of stripe rust resistance in a doubled haploid Canadian durum wheat population; and

iv. to determine whether the AM panel and the DH population contain previously un-identified genes for stripe rust resistance in durum wheat.

4 Materials and methods

4.1 Association mapping for stripe rust resistance

4.1.1 Plant material and experimental design

A collection of 92 diverse durum cultivars and breeding lines, obtained from major durum wheat breeding programs globally, were used in this project. In addition, three stripe rust susceptible checks (Avocet, Brigade and DT749) and two resistant checks (DT546 and Lillian) were included in the population. Three independent experiments (Table 3) were conducted where the population was inoculated with a collection of mixed isolates (MI) of stripe rust and two genetically uniform single isolates (W009 and W015). The MI were collected from susceptible spring wheat lines in Lethbridge, Alberta in August 2011, and the composition of the MI was unknown. Two other isolates: '152A' (W009) from Richardson, SK (50° 23.679N 104° 28.835W) and 'Foremost 2010 (leth) jz 3-12' (W015) from Lethbridge, AB, were obtained from naturally infected plants. To assess seedling resistance, these 96 accessions (including 4 checks, herein referred as the AM panel) were planted in the phytotron in an alpha-lattice design with three replications. For each experiment, the 96 accessions were planted in twelve blocks of eight accessions per block.

Table 3. Experimental design of three nurseries to assess seedling reaction to stripe rust in the association mapping population.

Stripe rust isolate	Collection	Experimental design	No. of replications	Checks	
				Susceptible	Resistant
MI	Lethbridge, AB	Alpha-lattice design	3	Brigade, DT749	Lillian, DT546
W009	Richardson, SK		3	Avocet, Brigade, DT749	Lillian, DT546
W015	Lethbridge, AB		3	Avocet, Brigade, DT749	Lillian, DT546

The AM panel was also planted in field disease nurseries at three locations over two years (Saskatoon, SK; Lethbridge, AB and Washington State University in 2012; Saskatoon; Lethbridge and Toluca in Mexico in 2013) to analyze adult plant

resistance to stripe rust. For this thesis, only Lethbridge and Toluca produced usable adult plant resistance data because the WSU site was lost to flooding. The data from Saskatoon was not used because there was little to no disease development (Table 4).

Table 4. Experimental design of three nurseries to assess adult plant reaction to stripe rust in the association mapping population.

Year	Location	Experimental design	No. of replications	No. of ratings	Checks	
					Susceptible	Resistant
2012	Lethbridge, AB	Un-replicated	1	1	DT532, 950090	Langdon, Flavio
2013	Lethbridge, AB	RCBD	3	1	Avocet	Lillian
2013	Toluca, Mexico	RCBD	3	3	Avocet, Brigade	Lillian, DT546

At Toluca, Mexico was conducted in a RCBD with three replications; the AM population was planted in single row plots of 1.5 meters, separated by 0.5 meters, on June 5th, 2013. The Lethbridge stripe rust nursery was seeded with three replications in 2012, but two replications were lost because of flooding. The AM panel was planted in rows of 20 seeds with 1 meter spacing among rows. The trial in Lethbridge 2013 was conducted in a RCBD with three replications. For the field trial in Lethbridge, the collection of mixed *Pst* isolates collected from fields of western Canada in 2011 was increased in the phytotron during the winter, and was subsequently used as inoculum in 2012. In 2012, multiple isolates collected in western Canada were increased in the phytotron, and then used as inoculum in 2013. For the field trial in Toluca, Mexico, the freshly multiplied inoculum from a mixture of virulent *Pst* races from Mexico was used to inoculate the field trial.

In Lethbridge, two to three inoculations were applied on the spreader rows over 7 days when the wheat spreader rows reached the three to four leaf stages. The isolates of *Pst* were suspended in light mineral oil (Bayol®, Esso Canada, Toronto, ON.), at a concentration of 0.5 g of urediniospores per 500 ml of Bayol, and sprayed onto spreader rows with a Herbiflex sprayer (Micron Sprayers Ltd., Bromyard, UK). After the Bayol evaporated, the spreader rows were wetted with distilled water and covered with dark plastic tarp for up to 24 hours to promote infection. For the field trial in Toluca, Mexico, inoculation was done on the spreader rows and also on each plot up to three times.

4.1.2 Analysis of stripe rust reaction

In the phytotron evaluation of resistance, seedlings were planted in a rust-free environment (University of Saskatchewan) with a diurnal temperature cycle of 18°C/22°C with a photoperiod of 8 h darkness and 16 h light. Seedlings at the two-leaf stage (approximately 10 days after planting) were inoculated with MI of stripe rust. The MI were collected from susceptible spring wheat lines in Lethbridge, Alberta in August 2011. The urediniospores were suspended in Bayol at a concentration of 0.01 g of urediniospores per 900 µl. After inoculation with an air-compressor above plants, the seedlings were left to dry and transferred to a dew chamber (10°C) and kept in darkness for 24 hours. Seedlings were then moved to a growth chamber at 10°C/15°C with a photoperiod of 8 h of darkness and 16 h of light (Cheng and Chen, 2010). Infection type (IT) data were recorded (first and second leaf) 10-18 days after inoculation based on the 0 (resistant) - 9 (susceptible) scale (Table 5). Disease severity was scored twice (approximately two days apart). Scoring_1 and Scoring_2 were analyzed independently.

Table 5. Major infection type classes for seedling stripe rust rating (Singh and Saari, 1992; McIntosh, et al., 1995).

Infection Type (McNeal, 1971)	**Host Response**	**Symptoms**
0	Immune	No visible uredia
1	Very resistant	Necrotic flecks
2	Resistant	Necrotic areas without sporulation
3-4	Resistant	Necrotic and chlorotic areas with restricted sporulation
5-6	Moderately resistant	Moderate sporulation with necrosis and chlorosis
7-8	Moderately susceptible	Sporulation with chlorosis
9	Susceptible	Abundant sporulation without chlorosis

Following the same method, two other isolates: ‘152A’ (W009) from Richardson, SK (50° 23.679N 104° 28.835W) and ‘Foremost 2010 (leth) jz 3-12’ (W015) from Lethbridge, AB, obtained from naturally infected plants were used to inoculate the AM population in the phytotron.

For field evaluation, reaction to stripe rust was screened for all checks and experimental lines using the modified Cobb scale (Table 6). Three times ratings were used to measure area under the disease progress curve (AUDPC) for the field data collected from Mexico. The first rating was performed when the flag leaves of susceptible checks reached 40% severity, and the subsequent ratings were performed every five days with the final rating when the susceptible checks were at 100% severity, at approximately Zadoks growth stage (GS) 55 (Vazquez, et al., 2012; Zadoks, et al., 1974). The AUDPC was calculated using a 1% to 100% scale of Buerstmayr (2000) $\text{AUDPC} = \sum_{i=1}^{n}\left[\frac{Y_i + Y_{i-1}}{2}\right](T_i - T_{i-1})$

Where: n is the total number of ratings, Y_i is the stripe rust severity for the ^{i}th rating and T_i is the day of the ^{i}th rating.

Table 6. The modified Cobb scale (Peterson, et al., 1948).

Actual percent leaf infected	0.37	1.85	3.70	7.40	11.1	14.80	18.50	22.20	25.90	29.60	33.30	37.00
Modified Cobb rating	1	5	10	20	30	40	50	60	70	80	90	100

4.1.3 Phenotypic data analysis

Data were analyzed using PROC MIXED in SAS V9.3 with accessions as a fixed effect, while replications (Rep) and blocks nested within replications [Block (Rep)] were considered random. The least square (LS) means for the stripe rust rating data were calculated using LS MEAN in SAS V9.3 (Littell, et al., 1996). Because LS means of the rating data were continuous data, histograms were used to assess the normality of the data (Pescatello and Roth, 2011). If the LS means did not resemble a normal distribution, several methods of transformation (log, square root, reciprocal) were performed and the data re-assessed using histograms. The normally distributed data were reanalyzed using PROC MIXED as above. Pearson's correlation coefficient among least square means for each rating time was estimated using EXCEL V2010.

4.1.4 Marker data analysis

Genomic DNA of plant materials was extracted from leaves of one-week-old seedlings using the cetyl trimethylammonium bromide (CTAB) protocol (Dvorak, et al., 1988). Standard gel electrophoresis using a 1.5% (w/v) agarose gel with known size standards was used to evaluate the quality and integrity of the DNA samples. The PicoGreen fluorometric assay (Singer, et al., 1997) was applied to quantify the DNA.

A 90K SNP (containing 81,587 SNP markers) Infinium iSelect assay (Wang, et al., 2014) was used to complement data from 244 SSR markers was already available for this population (Reimer, 2008). Ten microliters of 50 ng/µl DNA of each sample was used for genotyping with the 90K SNP assay. Infinium genotyping data were analyzed using the genotyping module of Illumina GenomeStudio data analysis software GSGT, version 1.9.4 (Illumina, San Diego, CA). Each line of the AM population was initially genotyped using the standard cluster file from Illumina; using these clusters as a starting point, a genotyping quality control (QC) process was applied to create a new cluster file for the lines of the AM population. A sequence of filters (Table 7) was used to remove SNP calls of low quality.

Table 7. The sequence of filters set up to remove false-positive SNP calls. GenomeStudio software program was used.

Steps	Filters	Description	Threshold to keep markers	Num. of SNPs left
1	Allele Freq.	Remove all monomorphic markers	Allele frequency < 1	48,248
2	Cluster Sep.	Cluster separation – genotypic clusters separated into two discrete groups	Cluster Sep >= 0.2	47,830
3	Call Freq.	Removal of SNP markers with > 5% missing data	Call Freq >= 0.95	36,813
4	AB R Mean	Remove SNP markers with low signal intensity	AB R Mean >= 0.2	36,618
5	AB T Mean	Remove SNP markers where AB clusters has shifted toward the AA or BB	0.2 < AB T Mean < 0.8	35,175
6	Minor Freq.	Removed markers with a minor allele frequency of less than 10%	Minor Freq >= 0.1	13,539

4.1.5 Population structure

Three approaches were used to estimate population structure within the AM population: i, distance-based phylogenetic analysis using PowerMarker v.3.25; ii, principle component analysis using TASSEL V3.0 (Kang, et al., 2010); and iii, model-based Bayesian clustering approach using STRUCTURE V2.3.4 (Falush, et al., 2003). The allele frequency-based distances were estimated based on Rogers' Euclidean distance (Rogers, 1972) and were used to construct a phylogenetic tree following the un-weighted pair-group method using arithmetic average (UPGMA) algorithm. A bootstrap test with 1,000 replications was utilized to reconstruct the tree by randomly sampling the data with replacement; a list of tree outputs was summarized to obtain a consensus tree by the program CONSENSUS in the PHYLIP V3.6 package (Felsenstein, 2005), using Extended Majority Rule. The consensus phylogenetic tree was displayed on the tree generator iTOL V2.2.2 (Letunic and Bork, 2011); bootstrapping values of the branches were assigned at the branch nodes (Felsenstein, 2005).

Principle component analysis (PCA) was performed with the program TASSEL V3.0 for 13,539 SNP markers. For numeric genetic data, the default method Correlation was set up with three PCA axes. The PCA results were plotted using SigmaPlot V12.0 (Systat Software, Inc., San Jose California USA, www.sigmaplot.com). In addition, a Bayesian model-based clustering approach was also used to infer population structure based on genotype data consisting of 28 unlinked SSR markers using the program STRUCTRE V2.3.4. The 28 unlinked SSR markers (one marker from each chromosome arm, Appendix 3) selected from 245 microsatellite markers based on the polymorphism information content (PIC) value (Botstein, et al., 1980) was determined by the program PowerMarker V3.25 (Liu and Muse, 2005). An allele frequency independent model with 10,000 burn-in period and 100,000 Markov chain Monte Carlo (MCMC) replications after burn-in was applied in STRUCTURE. For each "K" (number of sub-populations) from 1 to 12, 20 independent runs were completed to quantify the variation of likelihood of each K. The average of log likelihood was estimated as posterior probability, and using the second order rate of change of log likelihood, the ad hoc quantity ΔK was estimated by STRUCTURE HARVESTER (Evanno, et al., 2005; Earl, 2012). The coefficient of

membership of lines within each sub-population was assigned in STRUCTURE for the optimal number of clusters as a Q matrix.

Since several factors can influence clustering, including size of the population, and the number of markers (Rosenberg, et al., 2005). It is not unusual to observe multiple peaks on the curve of ΔK value with respect to K, and in those cases, the K value that captures the majority of the structure and can be explained biologically is most appropriate (Moore, et al., 2013). In this thesis, the ΔK value peaked at K = 2, 3 and 5. However, based on the PCA, distance-based analysis, and current pedigree information, the most likely number of sub-populations was K = 3 or K = 5. Because it was not possible to determine the best of these two, the association analysis was performed twice, using the Q matrix as covariate at K = 3 and K = 5 (Appendices 7, 8 and 9). A Q-Q ("Q" stands for quantile) plot was used to compare associations estimated using the two Q matrices (Riedelsheimer, et al., 2012).

4.1.6 Marker-trait associations

Marker-trait associations were tested with a mixed linear model (MLM) within the program TASSEL V3.0 using LS means from each rating, the Q matrix estimated for K = 3 and K = 5 was used as a covariate, and pairwise kinship coefficients considered random. Associations were considered significant if $P < 0.05$ after correction for multiple testing using 1,000 permutations of GLM and using a positive false discovery rate (FDR) method of MLM to confirm (Storey, 2002; Storey and Tibshirani, 2003), the FDR *Q* value was calculated using R package 'fdrtool'.

The linkage disequilibrium between pair-wised markers was calculated using TASSEL V3.0. LD was measured using the squared correlation between a pair of loci (r^2), and was plotted against genetic distance between adjacent markers. The LD decay against genetic distance was simulated in a nonlinear regression model (Hill and Weir, 1988), where:

$$r^2 = \{(10 + x)/[(2 + x)(11 + x)]\} * \{1 + \frac{(3 + x)(12 + 12x + x^2)}{[n(2 + x)(11 + x)]}\}$$

x was genetic distance (cM) between pair-wised markers and n was the association mapping population size. The critical r^2 value referred to the 95% quantile of r^2

values between unlinked SNP markers (markers located at different chromosomes). The positions of SNPs were determined according to the consensus durum wheat constructed by Maccaferri, et al. (2014).

4.2 Genetic mapping of seedling stage stripe rust resistance

4.2.1 Plant material and trait evaluation

To study the genetics of resistance, a well genotyped DH population derived from the cross Kofa/W9262-260D3 was used to evaluate the seedling resistance to single isolates, and APR in the field. The mapping population consisted of 155 F_1-derived DH lines developed from the cross Kofa x W9262-260D3 using the maize pollen method (Clarke, et al., 2002). W9262-260D3 is an F_9 inbred line from the cross Kyle*2/Biodur made in the Agriculture and Agri-Food Canada-Swift Current breeding program, and Kofa is a US semi-dwarf cultivar developed by West-Bred, LLC (Clarke, et al., 2002; Pozniak, et al., 2007). This population has been characterized extensively for stem solidness (Clarke, et al., 2002), endosperm color (Clarke, et al., 2006; Pozniak, et al., 2007), kernel weight, test weight (Houshmand, et al., 2008) and grain cadmium concentration (Knox, et al., 2009; Wiebe, et al., 2010)

The DH population and the two parents were planted and evaluated in the phytotron at University of Saskatchewan and in the field at Lethbridge, AB using an alpha-lattice design with three replications (in 2013, but only Lethbridge had adult plant resistance data) (Table 8). Single isolates W009 and W015 were used to inoculate the DH population under controlled conditions (Table 9). The inoculation and rating methods were described in section 4.1.2.

Table 8. Experimental design of one nursery to assess adult plant reaction to stripe rust in the DH population.

Year	Location	Experimental design	No. of replications	No. of ratings	Checks	
					Susceptible	Resistant
2013	Lethbridge, AB	Alpha-lattice	3	1	Avocet, Kofa, Westbred881	Lillian, W9262-260D3

Table 9. Experimental design of two nurseries to assess seedling reaction to stripe rust in the DH population.

Stripe rust isolate	Collected from	Experimental design	No. of replications	Checks	
				Susceptible	Resistant
W009	Richardson, SK	Alpha-lattice design	3	Avocet, Kofa	W9262-260D3

For the phenotypic data collected from the phytotron, the distribution of the individual ratings indicated the putative presence of two major genes. The phenotypic ratings were used as phenotypic data for QTL mapping.

Genomic DNA of seedlings of the DH population and parents was extracted using the CTAB protocol. A 90K SNP Infinium iSelect assay, 109 SSR markers and 125 DArT markers were analyzed in the DH population. A genetic map of the DH population was constructed using MSTMap by Dr. Amidou N'Diaye (University of Saskatchewan) (Wu, et al., 2008) and MapDisto V1.7.7 (Lorieux, 2012).

4.2.2 Statistical analysis and QTL analysis

The phenotypic data were analyzed using PROC MIXED in SAS V9.3 with accessions as a fixed effect, while replications (Rep) and blocks nested within replications [Block (Rep)] were considered random. Data were subjected to standard analysis of variance (ANOVA). Also, the phenotypic ratings were transformed into binary data based on the IT scores. Individuals with IT scores of 0-4 and 4-9 were scored as 0 (resistant) and 1 (susceptible), respectively. The deviations of observed and expected frequencies of resistant individuals in G9586 were tested using a Pearson's Chi-squared test (Preacher, 2001). QTL mapping using the constructed genetic map was performed with the composite interval mapping (CIM) procedure of Qgene V4.3.10 (Joehanes and Nelson, 2008). For CIM, the method of stepwise cofactor selection was applied; the maximum number of cofactors, F to add and F to drop were selected automatically. To determine the critical LOD thresholds for CIM, permutations of 1,000 iterations were applied at a significance level of 0.01. The permutation LOD of 0.01 was used to declare the significance of QTLs. Significant QTLs were illustrated with diagonally hatched bars using MapChart V2.2 (Voorrips,

2002). The additive and epistatic effects of QTLs were investigated using SAS V9.3 based on QTL identified using the CIM.

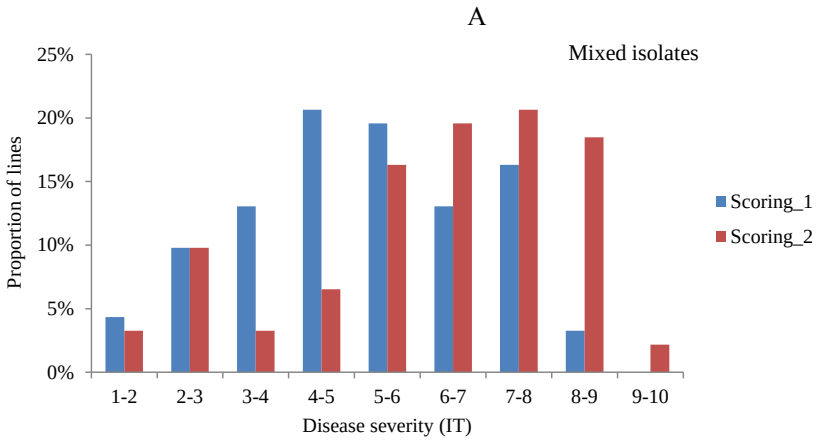
When multiple QTLs were identified at locations adjacent to each other, meta-analysis was used to determine if they were a single locus (Liu, et al., 2009; Hanocq, et al., 2007). In this study, BioMercator V4.2 software was used in QTL meta-analysis, and to illustrate co-locations between two QTLs (Arcade, et al., 2004; Veyrieras, et al., 2007). In a previous study of hexaploid wheat, it was reported that two QTLs could be considered a single QTL when LOD peaks were within 20 cM of each other (Asad, et al., 2014).

5 Results

5.1 Association mapping of stripe rust resistance

5.1.1 Phenotypic data

In the seedling test using the MI, the LS means for the first rating (Scoring_1) followed a normal distribution and disease severity ranged from 1.37 to 8.33 (Figure 2A) in the AM population. The LS means of Scoring_2 was skewed towards higher severities and ranged from 1.71 to 9.12. For the seedling test using the single isolate W009, the LS means of Scoring_1 ranged from 1.35 to 7.73 (Figrue 2B) and from 1.57 to 7.72 for the second rating. For the seedling test using single isolate W015, the LS means of Scoring_1 and Scoring_2 ranged from 1.80 to 6.91 and from 2.05 to 7.31, respectively (Figure 2C, Appendix 5). For the field trials, the distribution of Leth2012_AM, LS means of Leth2013_AM, AUCPC for Mexico2013 and transformed AUDPC are plotted in Figures 3A, 3B, 3C and 3D, respectively. They shared the same distribution, where a high proportion of the AM population had low disease severity (Appendix 6). The AUDPC for Mexico2013 followed a normal distribution after square-root transformation (Figure 3D), however, Leth2012_AM or Leth2013_AM didn't follow normal distribution after the square-root transformation.



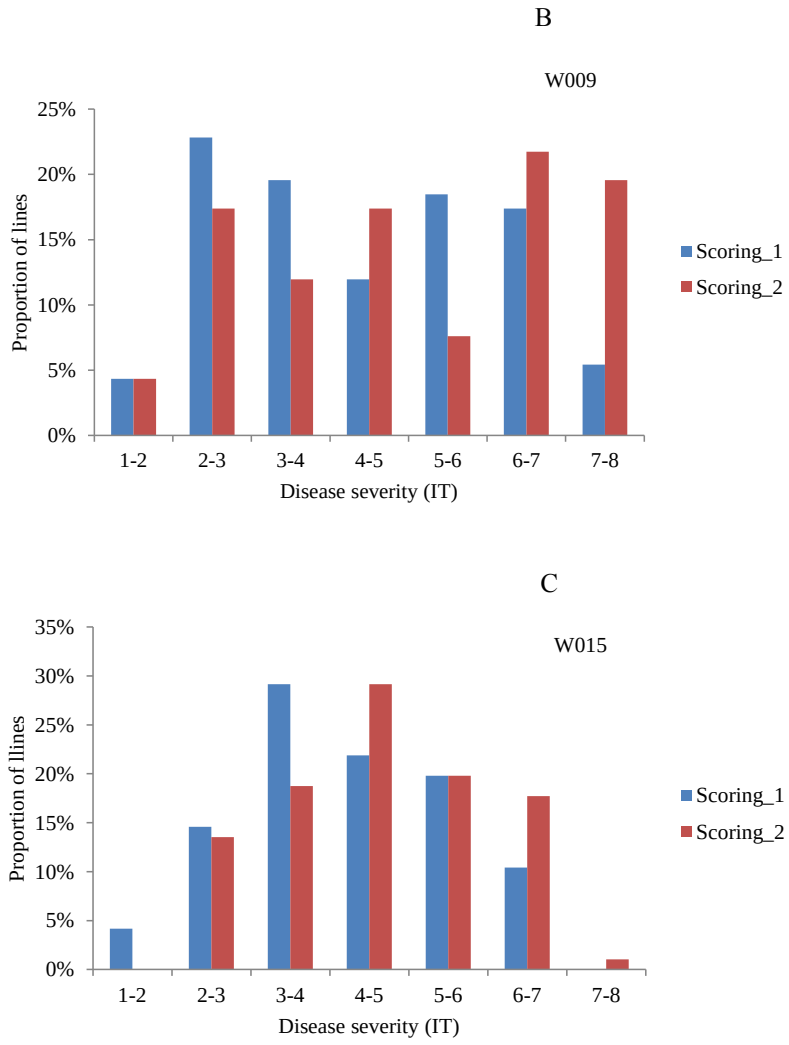
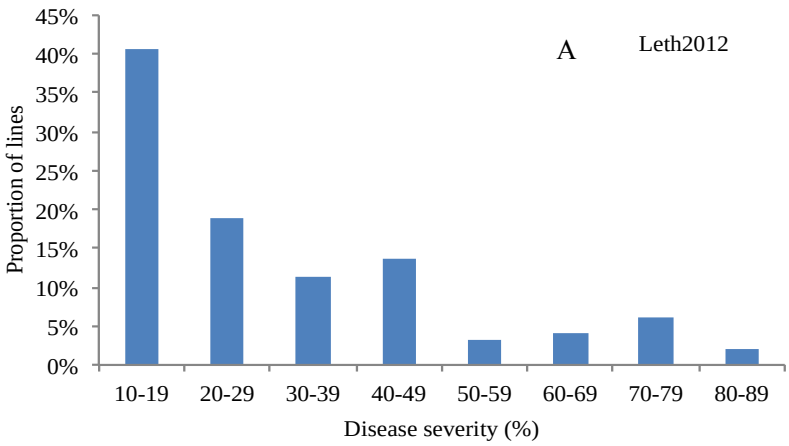
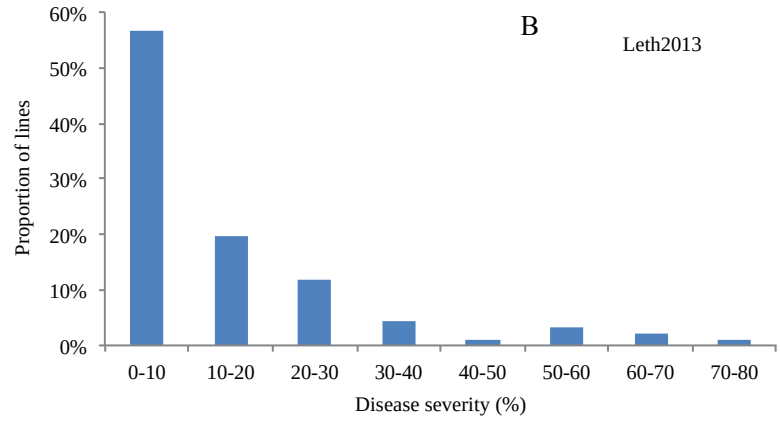
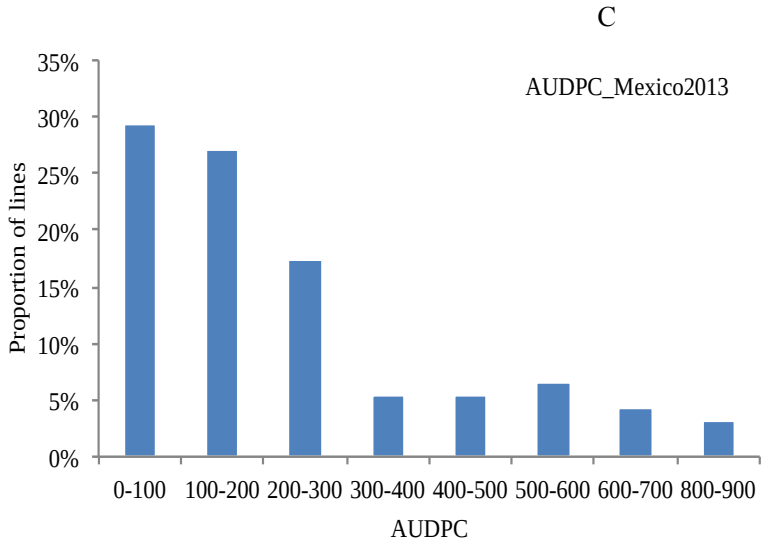


Figure 2. (A) Frequency distribution in the AM population for response to seedling stripe rust with (A) MI, (B) single isolate W009 and (C) W015. Data of two assessments scored at 12 days (Scoring_1) and 15 days (Scoring_2) after inoculation.







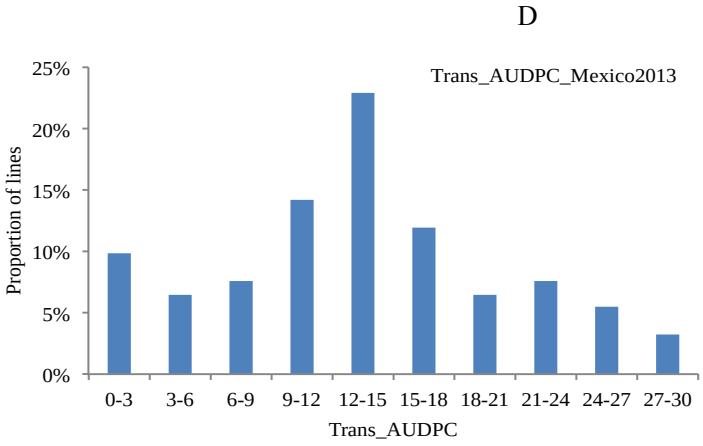


Figure 3. Assessment of AM population, for stripe rust disease severity at Lethbridge 2012 and 2013 (A and B) and AUDPC in Mexico 2013 untransformed (C) and square-root transformed (D).

Analysis of variance (ANOVA) was conducted for all phenotypic data consisting of three replications, including LS means of two time ratings of MI, W009 and W015, adult plant resistance in Lethbridge 2013 and transformed AUDPC data in Mexico 2013 (Tables 10 and 11). The ANOVA test revealed significant differences ($P < 0.001$) among accessions for both Scoring_1 and Scoring_2 of seedling resistance to MI, and single isolates W009 and W015, as indicated by the F-test (Table 10). For the transformed AUDPC_Mexico2013 and Leth2013_AM, the ANOVA test showed that the accessions were also significant ($P < 0.001$) (Table 11).

Table 10. Variance estimates for random effects and F-values for fixed effects from ANOVA for two assessments (Scoring_1 and Scoring_2) of AM panel seedling resistance to MI, W009 and W15, data was analyzed using PROC MIXED in SAS.

Effect	Seedling resistance to stripe rust					
	MI		W009		W015	
	Scoring_1	**Scoring_2**	**Scoring_1**	**Scoring_2**	**Scoring_1**	**Scoring_2**
	RANDOM EFFECTS VARIANCE ESTIMATES					
Rep	0.312	0.101	0.121	0.0073	0.118	0.112
Block (Rep)	0.338**	0.157*	0.0576	0.0943	0.181**	0.179**
Residual	0.920***	0.818***	0.763***	0.682***	0.416***	0.485***
	FIXED EFFECT F-VALUES					
Accession	9.450***	13.310***	10.660***	14.870***	11.190***	10.520***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Table 11. Variance estimates for random effects and F-values for fixed effects from ANOVA, square-root transformed AUDPC in Mexico 2013 and disease severity Leth2013_AM of adult plant resistance reaction in the AM population.

	Adult plant resistance to stripe rust	
Effect	**Trans_AUDPC_Mexico2013**	**Leth2013_AM**
	RANDOM EFFECTS VARIANCE ESTIMATES	
Rep	0.095	1.061
Block (Rep)	6.218***	174.25***
Residual	0.877	0.994
	FIXED EFFECT F-VALUES	
Accession	24.99***	4.64***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

The LS means of the two rating times were positively correlated (r = 0.907, $P <$ 0.001) for both the MI and W009 (Table 12). Also, rating times (Scoring_1 and Scoring_2) were highly correlated for disease severity of MI and W009. For the field data, Leth2013_AM and AUDPC_Mexico2013 were highly correlated, but the correlation between each of these trials and Leth2012_AM was low to moderate (r = 0.369, $P < 0.001$ and r = 0.314, $P < 0.001$) (Table 13). The correlations among the phenotypic data used in the association analysis are listed in Table 14.

Table 12. Pearson correlations among LS means for Scoring_1and Scoring_2 seedling reactions to MI, and single isolates W009 and W015, within the AM population.

	Scoring_1_MI	Scoring_2_MI	Scoring_1_W009	Scoring_2_W009	Scoring_1_W015	Scoring_2_W015
Scoring_1_MI	1					
Scoring_2_MI	0.926***	1				
Scoring_1_W009	0.868***	0.878***	1			
Scoring_2_W009	0.853***	0.907***	0.962***	1		
Scoring_1_W015	0.805***	0.757***	0.795***	0.746***	1	
Scoring_2_W015	0.788***	0.774***	0.801***	0.770***	0.974***	1

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Table 13. Pearson correlations among LS means for adult plant resistance in the field for three time points (19-Aug-2013, 27-Aug-2013 and 03-Sep-2013) and AUDPC in Mexico 2013, Leth2012_AM and Leth2013_AM within the AM population.

	19Aug2013_Mexico	27Aug2013_Mexico	03Sep2013_Mexico	AUDPC_Mexico2013	Leth2012_AM	Leth2013_AM
19Aug2013_Mexico	1					
27Aug2013_Mexico	0.978***	1				
03Sep2013_Mexico	0.957***	0.988***	1			
AUDPC_Mexico2013	0.983***	0.999***	0.992***	1		
Leth2012_AM	0.290**	0.308**	0.333**	0.314**	1	
Leth2013_AM	0.715***	0.731***	0.747***	0.738***	0.369***	1

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Table 14. Pearson correlations among phenotypic data collected for the AM population.

	AUDPC_ Mexico2013	Leth2012_AM	Leth2013_AM	Scoring_2_MI	Scoring_2_W009	Scoring_2_W015
AUDPC_Mexico2013	1					
Leth2012_AM	0.314**	1				
Leth2013_AM	0.738***	0.369***	1			
Scoring_2_MI	0.623***	0.183	0.454***	1		
Scoring_2_W009	0.584***	0.127	0.400***	0.907***	1	
Scoring_2_W015	0.701***	0.202	0.421***	0.774***	0.770***	1

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

The phenotypic data for the AM panel is presented in Appendices 5 and 6, but is summarized for discussion purposes (Table 15). In the AM panel, the majority of Canadian germplasm were susceptible to stripe rust at the seedling stage. In fact, Strongfield and CDC Verona, the two prominent cultivars currently grown in Western Canada had an IT > 4, although CDC Verona was resistant to isolate W009 (Table 15). DT696, which has been suggested as a source of fusarium head blight (FHB) resistance, had a high IT for the MI and isolate W015, and moderate a IT to isolate W009 (Table 15). Interestingly, some breeding lines, such as DT707, were susceptible at the seedling stage, but had a low disease severity score in field trials at Lethbridge and Mexico. These results suggest that some lines may carry APR genes.

Table 15. List of 15 accessions and 24 Canadian cultivars in the AM panel, their seedling reaction to MI, and single isolates W009 and W015, and their adult plant reaction in Lethbridge and Mexico 2013. Seedling reaction with IT > 4 and adult plant resistance with disease severity > 20% is indicated in bold.

Accession	Origin	MI	W009	W015	Leth2013_AM	03sep2013_Mexico
Buck Ambar	Argentina	1.7	1.8	2.1	5.0	0.0
Carioca	France	1.8	1.6	2.2	5.0	3.3
Durabon	Germany	3.5	2.4	3.2	5.0	3.3
D-73-15	Iran	2.4	2.6	2.9	5.0	1.7
Arcobaleno	Italy	2.3	2.2	2.1	5.0	0.0
Ciccio	Italy	3.8	3.0	3.6	8.3	3.3
Iride	Italy	2.7	2.1	2.1	5.0	0.0
Parsifal	Italy	2.0	2.1	2.1	5.0	8.3
Tresor	Italy	2.3	2.8	3.2	8.3	0.0
DHTON 1	Morocco	3.2	2.7	3.2	5.0	3.3
Arrivato	New Zealand	1.8	1.6	2.2	5.0	0.0
CFR5001	New Zealand	2.8	2.4	2.7	5.0	3.3
CRDW17	New Zealand	1.9	2.0	3.2	5.0	3.3
Altar-Aos	Spain	3.9	2.7	2.3	5.0	1.7
Gallareta	Spain	1.8	2.2	2.1	5.0	5.0
9661-AF1D	Canada	**7.2**	**5.9**	**5.2**	18.3	11.7
9661-CA5E	Canada	**6.3**	**4.3**	3.6	5.0	1.7
AC Avonlea	Canada	**5.0**	**4.5**	3.9	5.0	8.3
AC Melita	Canada	**7.9**	**6.1**	**4.5**	**38.3**	**26.7**
AC Morse	Canada	**8.3**	**7.1**	**6.8**	8.3	**46.7**
AC Napoleon	Canada	**4.3**	2.2	**4.7**	15.0	13.3
AC Navigator	Canada	**8.8**	**7.6**	**7.3**	**21.7**	**50.0**
AC Pathfinder	Canada	**8.9**	**7.6**	**6.1**	**71.7**	**70.0**
Commander	Canada	**7.5**	**6.6**	**6.8**	18.3	**33.3**
D24-1773	Canada	**5.9**	**5.3**	**4.6**	**41.7**	13.3
DT513	Canada	**6.9**	**4.6**	**4.2**	5.0	8.3
DT536	Canada	**8.9**	**7.3**	**6.9**	15.0	**33.3**
DT691	Canada	**5.9**	3.3	**4.2**	11.7	**33.3**
DT695	Canada	**5.8**	2.5	3.9	**51.7**	**50.0**
DT696	Canada	**5.8**	3.4	**6.1**	5.0	20.0
DT704	Canada	**8.2**	**7.0**	**6.5**	5.0	**30.0**
DT705	Canada	**5.1**	3.6	**4.2**	5.0	1.7
DT707	Canada	**4.3**	**4.2**	**4.3**	5.0	0.0
DT709	Canada	**8.0**	**6.8**	**6.1**	11.7	**43.3**
DT710	Canada	**6.5**	**4.3**	3.9	**21.7**	6.7
DT711	Canada	**7.6**	**6.5**	**6.3**	18.3	15.0
Kyle	Canada	**5.4**	**4.7**	**4.8**	11.7	15.0
Strongfield	Canada	**6.4**	**4.5**	**5.2**	**51.7**	18.3
CDC Verona	Canada	**5.2**	3.6	**5.7**	5.0	8.3
Average LSD $_{0.05}$	/	0.8	0.7	0.6	10.8	4.1

There were fifteen accessions in K=5_Pop2 that were resistant (IT < 4) to MI, and to single isolates W009 and W015 at the seedling stage, and their disease severities were less than 9% in the field (Lethbridge and Mexico 2013) at the adult plant stage. The majority of these cultivars were from Argentina, France, Germany, Iran, Italy, Morocco, New Zealand and Spain (Table 15). Given the high level of resistance observed in these lines, they may be a useful source of resistance that can be used by Canadian durum wheat breeders to improve resistance.

5.1.2 Marker data analysis

A total of 92 accessions were collected from 13 countries, predominantly Canada, Italy, and USA, which were genotyped using a SNP array containing 90K SNPs. Before filtering the SNP data, the reliability and call rate of DNA samples were checked. Samples with low genotype call reliability (Gencall Score < 0.181) and call rate (call rate < 0.84) were removed, and newly extracted DNA samples were re-genotyped until the quality met the standard. Table 7 indicated the steps used to filter the SNPs of the 81,587 markers, 40.9% were removed because they were monomorphic; 0.5% (418) of the markers were removed because of poor cluster separation; 13.5% (11,017) of the markers with > 5% missing data were removed; 0.2% (195) of the markers were removed because of low signal intensity of potential heterozygous genotypes; 1.8% (1,443) of markers with AB clusters shifted toward AA or BB clusters were removed; 26.5% (21,636) with a minor allele frequency (MAF) of < 10% were removed. For the 13,539 SNPs remaining, the average polymorphism information content (PIC) was 0.292, ranging from 0.0975 to 0.375 with a peak frequency distribution between 0.360 and 0.375 (Figure 4).

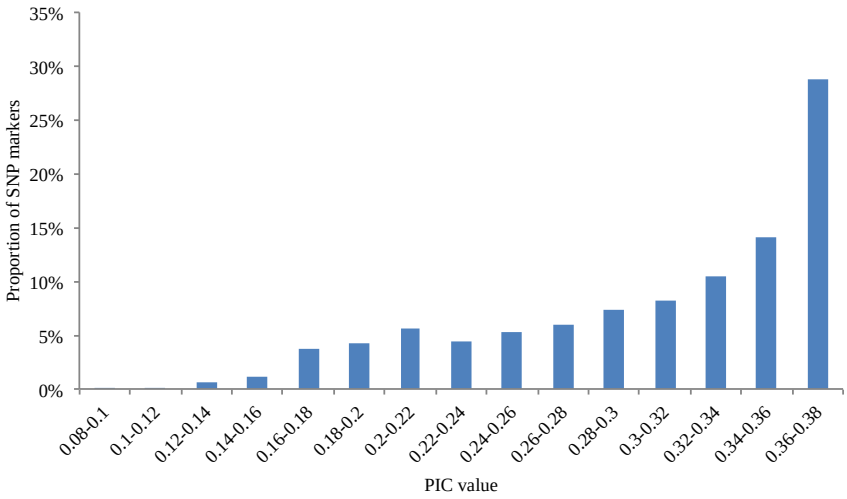


Figure 4. Frequency distribution of PIC value of 13,539 SNP markers.

The genetic positions of 12,237 SNPs of the 13,539 were determined according to the consensus map constructed by Maccaferri, et al. (2014). The 12,237 SNPs with known genetic positons were mapped to a total of 2,892 loci across 14 chromosomes (Table 16). On average, each chromosome contained 207 SNP loci, ranging from 165 on chromosome 4A to 272 on chromosome 2B. The consensus map based on the 12,237 polymorphic markers covered a total length of 2,570.2 cM, and chromosome sizes ranged from 131.1 cM (chromosome 6A) to 218.6 cM (chromosome 5A). The map did not have any gaps larger than 15 cM, and only six gaps larger than 10 cM (chromosomes 1B, 2A, 3B, 4A and 6A). The average resolution of whole genome was 1.13 SNPs / cM, ranging from 0.81 on chromosome 2A to 1.43 on chromosome 1B (Table 16).

Table 16. Mapping statistics for the SNP consensus map of durum wheat (Maccaferri, et al., 2014), consisting of 12,237 SNP markers.

Chromosome	Length (cM)	Num. of unique map positions	Density (Num. of markers/cM)	Max. gap (cM)	Num. of gaps larger than 10 cM
1A	149.0	181	1.21	9.50	0
1B	176.5	252	1.43	10.80	1
2A	212.5	173	0.81	12.20	2
2B	193.6	272	1.40	4.80	0
3A	184.3	169	0.92	7.10	0
3B	209.6	218	1.04	10.10	1
4A	177.3	165	0.93	10.50	1
4B	135.8	193	1.42	11.10	0
5A	218.6	183	0.84	6.70	0
5B	206.2	240	1.16	6.00	0
6A	131.1	184	1.40	11.10	1
6B	152.8	214	1.40	5.20	0
7A	210.6	222	1.05	6.10	0
7B	212.3	226	1.06	9.90	0
Whole genome	2570.2	2892	1.13	12.20	6

For linkage disequilibrium analysis in the association-mapping panel, only 12,237 out of 13,539 SNP markers were used for the analysis, because the locations of the other markers were unknown. The positions of those 12,237 markers were determined according to the durum wheat consensus map of Maccaferri, et al. (2014). The linkage disequilibrium value (r^2) was plotted against the genetic distance between markers located on the same chromosome (Figure 5). The critical r^2 value was 0.129 according to the 95% quantile pairwise r^2 value of SNP markers located at different chromosomes (unlinked SNP markers). The average genetic distance at which the r^2 fell below 0.129 was 5.9 cM.

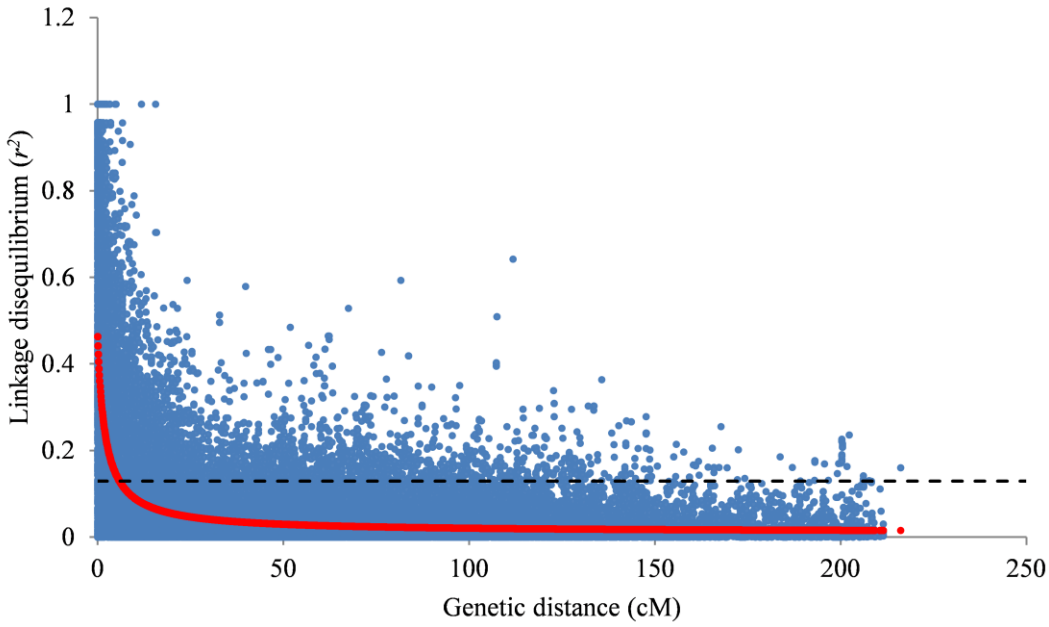
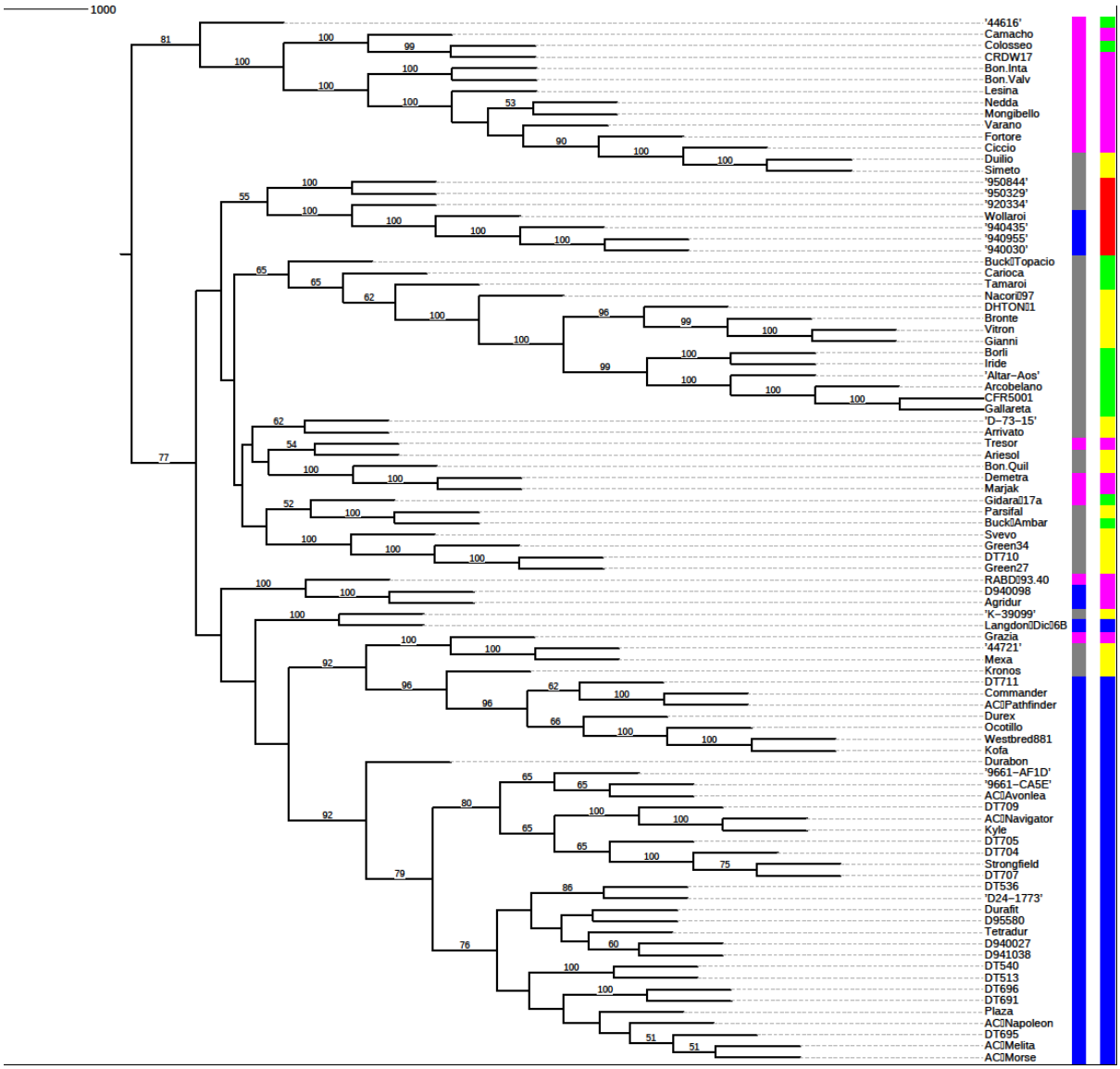


Figure 5. Linkage disequilibrium (r^2) decay plot of pair-wised markers as a function of genetic distance (cM) for the 92 AM accessions. The fitted curve indicated the expected LD decay between adjacent markers based on a nonlinear regression model. The critical r^2 value referred to the 95% quantile of r^2 value of unlinked SNP markers.

5.1.3 Genetic diversity and population structure

A phylogenetic tree was constructed based on the un-weighted Pair Group Method with Arithmetic Mean (UPGMA) clustering and Rogers' Euclidean distance, with bootstrapping analysis from 1,000 cycles of resampling (Figure 6A). Three or five major clusters could be identified in the phylogenetic tree. The AM population formed three or five clusters, which was consistent with their geographic origin (Figure 7), where the majority of North American and Australia accessions clustered in to single groups. The European and South American accessions were dismissed into multiple clusters, indicating a high degree of admixture among these populations.

(A)



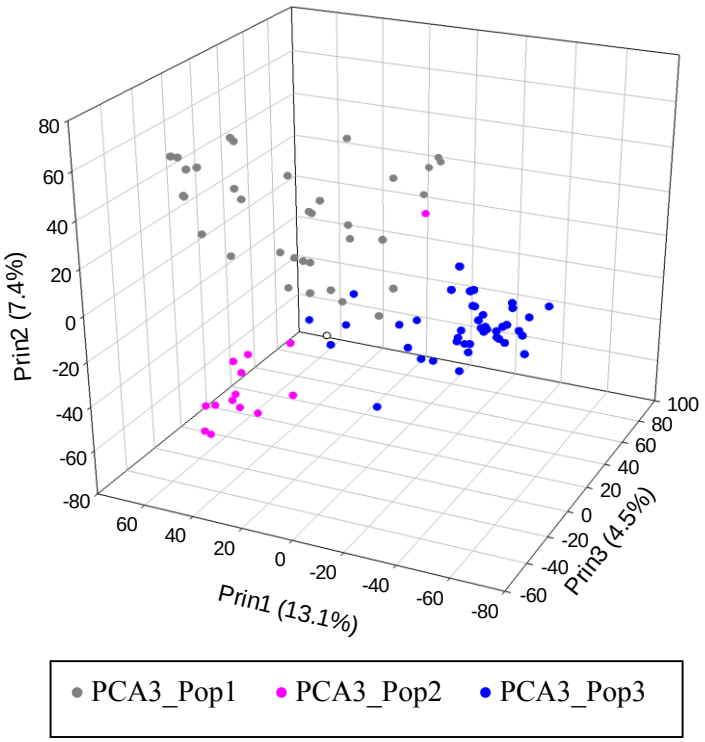
The 1st column:

● K=3_Pop1 ● K=3_Pop2 ● K=3_Pop3

The 2nd column:

● K=5_Pop1 ● K=5_Pop2 ● K=5_Pop3 ● K=5_Pop4 ● K=5_Pop5

(B)


Prin2 (7.4%)
Prin1 (13.1%)
Prin3 (4.5%)
PCA3_Pop1
PCA3_Pop2
PCA3_Pop3

(C)

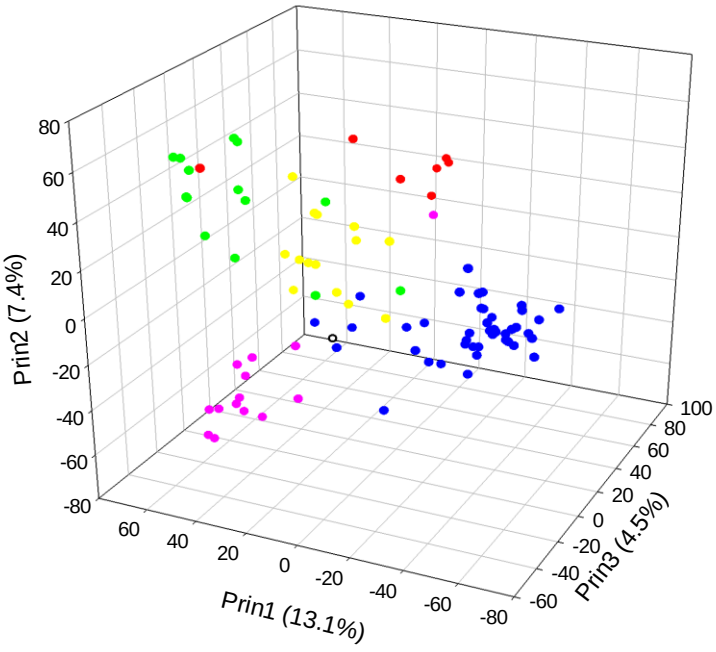
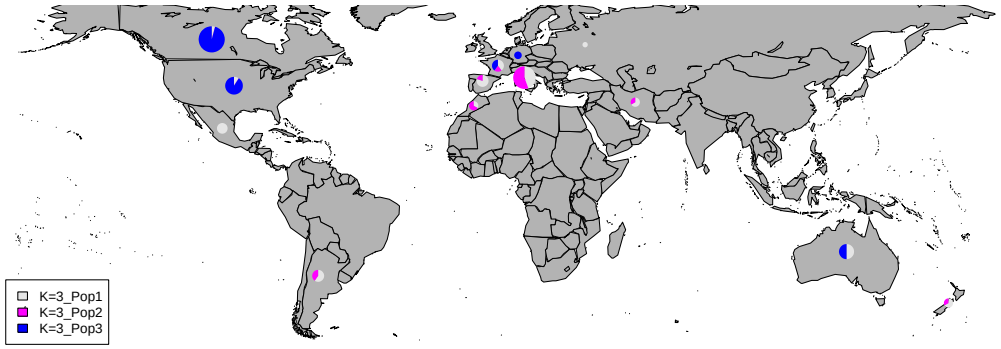

Prin2 (7.4%)
Prin1 (13.1%)
Prin3 (4.5%)
PCA5_Pop1
PCA5_Pop2
PCA5_Pop3
PCA5_Pop4
PCA5_Pop5

Figure 6. (A) Consensus UPGMA phylogenetic tree constructed using Rogers' Euclidean distance (Rogers, 1972) for the 92 durum wheat cultivars. Bootstrapping values > 50% from 1,000 cycles of resampling are shown at the internal nodes. The color strip on the left represents the composition of three sub-populations, the color strip on the right represents the composition of five sub-populations. (B) and (C) indicate the results of principal component analysis, each dot represents one of the 92 lines of the AM population in a space formed by Prin1, Prin2 and Prin3, the dots were colored according to the genetic distance-based classification.

(A)



(B)

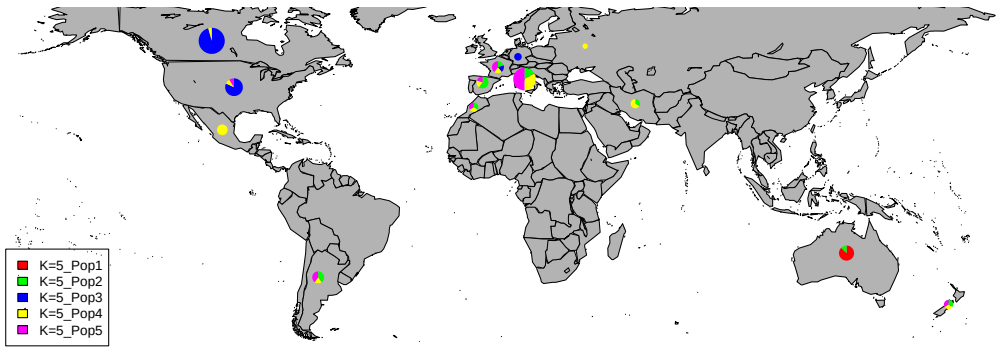


Figure 7. Country-specific distribution for sub-populations of K = 3 (A) and K = 5 (B) in the AM population. The radius of the pie chart is a reflection of the sample size and colors within each pie chart were a reflection of percentage of samples in each sub-population.

Population structure was further assessed using Bayesian analysis. For this analysis, 28 unlinked SSR markers were used and *a prior* sub-population sizes from 1 to 12 within the software STRUCTURE. Delta K peaked at K = 2, 3 and 5 (Figures 8A and B).

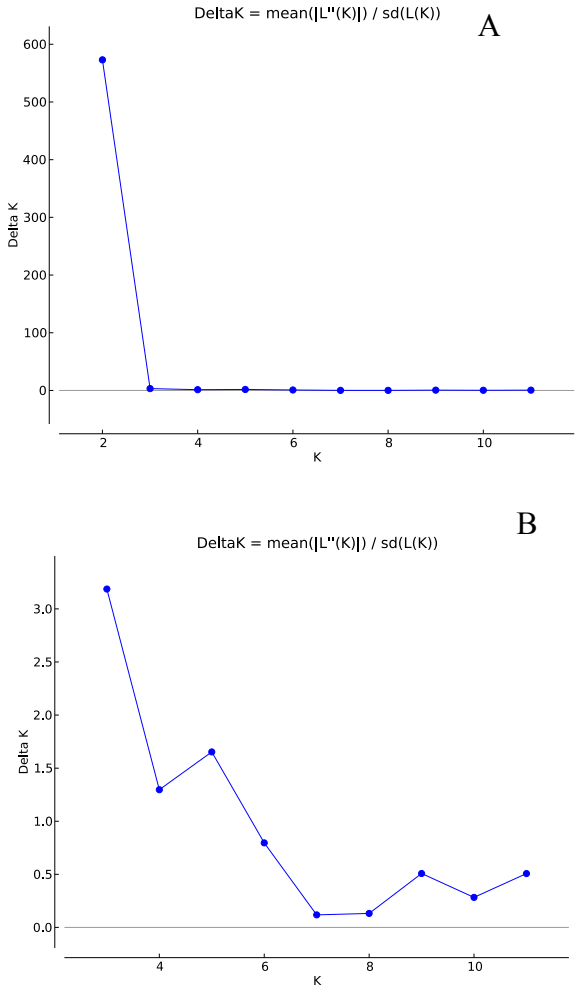


Figure 8. The *ΔK* indicating peaks of the *ΔK* value at K = 2 (A), 3 and 5 (B).

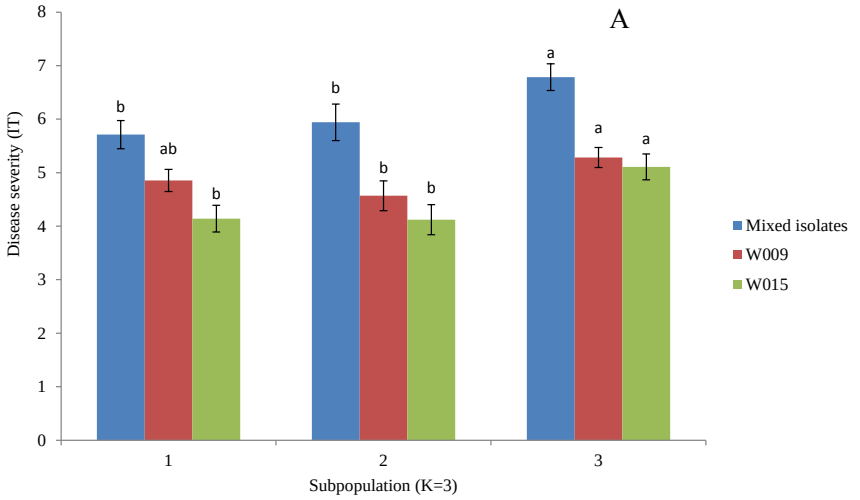
A principle component analysis (PCA) was conducted using all 13,539 SNP markers. This was consistent with the phylogenetic analysis, which revealed five sub-populations (Figure 6C). The first three principals explained 25.0% of the phenotypic variance, where Prin1, Prin2 and Prin3 explained 13.1%, 7.4% and 4.5%, respectively. Prin1 differentiated North American lines in the AM population; Prin2 differentiated a large part of the Italian lines, while Prin3 differentiated Australian lines.

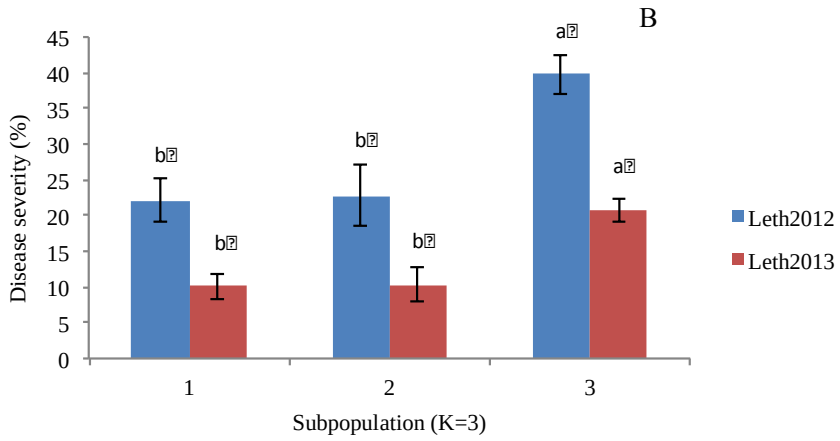
When considering five sub-populations (denoted as K=5_Pop1, K=5_Pop2, K=5_Pop3, K=5_Pop4 and K=5_Pop5 (Figure 6C), the sub-populations contained 8, 14, 38, 22 and 18% of the accessions, respectively (Appendix 7). All the Australian lines were grouped into K=5_Pop1 except Tamaroi. The accessions in the K=5_Pop2 were mainly from Argentina, Italy and Spain; the lines from Canada and US were

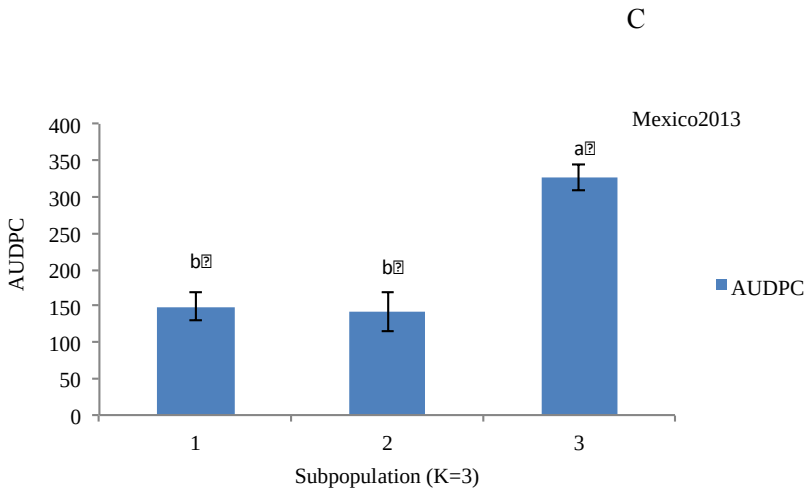
grouped together into K=5_Pop3, except DT710 and D940098. A Canadian accession, DT710, clustered with Green 27, which is not surprising given that Green 27 was a parent of DT710 (see pedigree information in Appendix 2). The lines in K=5_Pop4 were mainly from Italy, Mexico and Spain; and the lines in K=5_Pop5 were mainly from Italy (Figure 7, Appendix 7).

Based on all the analyses above, it appears that there are either three or five sub-populations. When the 92 accessions were divided into three sub-populations, K=5_Pop1, K=5_Pop2 and K=5_Pop4 clustered together, while K=5_Pop3 and K=5_Pop5 were independently clusters. Accessions in K=5_Pop5 were mainly from North America. Because it was not possible to easily differentiate between three or five sub-populations, association analysis was conducted using both K matrices.

For seedling tests using MI, the Least Significant Difference (LSD) test confirmed that there were significant differences ($P < 0.05$) in stripe rust severity among sub-populations (Figures 9 and 10). In the case of three sub-populations, the North American accessions, K=3_Pop3, had the highest average severity (6.8 ± 0.3), while K=3_Pop1 (5.7 ± 0.3) was not significantly different from K=3_Pop2 (5.9 ± 0.3). These results were consistent for the single isolate experiments. For the seedling test using isolate W009, accessions from K=3_Pop3 expressed the highest severity (5.3 ± 0.2), while accessions in K=3_Pop2 expressed the lowest (4.6 ± 0.3), but not significant lower than K=3_Pop1 (4.9 ± 0.2). For seedling resistance to isolate W015, K=3_Pop3 expressed the highest severity (5.1 ± 0.2), while accessions in K=3_Pop2 had the lowest (4.1 ± 0.3), but not significantly lower than K=3_Pop1 (4.1 ± 0.3) (Figure 9A).


A
Disease severity (IT)
Subpopulation (K=3)
Mixed isolates
W009
W015


B
Disease severity (%)
Subpopulation (K=3)
Leth2012
Leth2013


C
Mexico2013
AUDPC
Subpopulation (K=3)
AUDPC

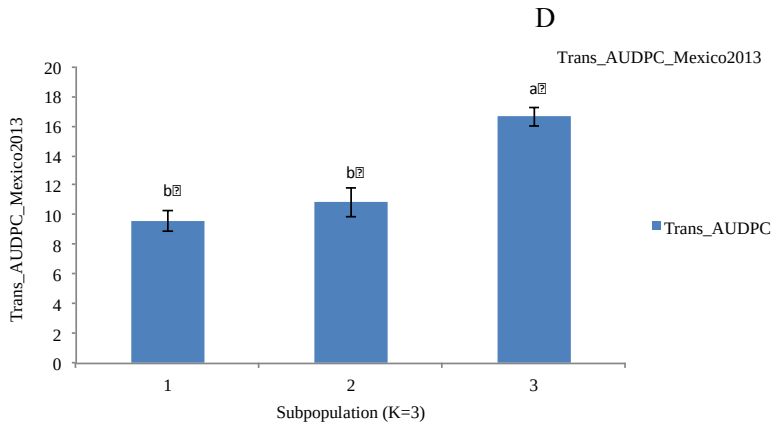
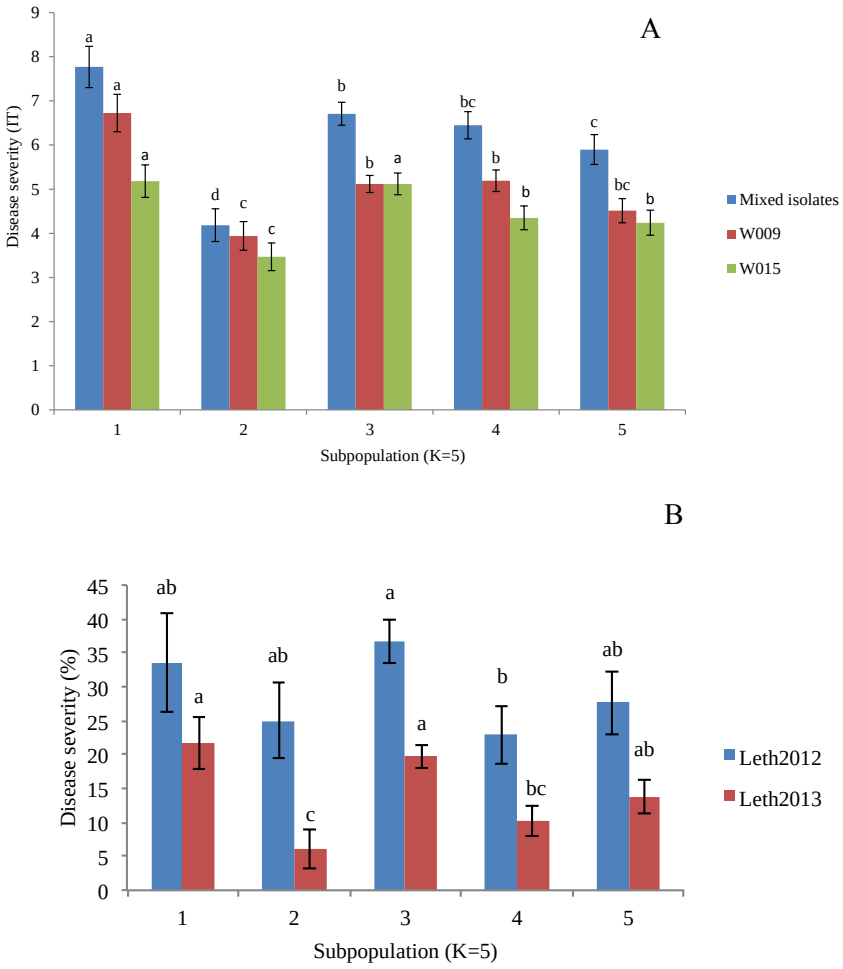


Figure 9. The second time point scorings in three durum wheat subpopulations inoculated with (A) MI, single isolate W009 and W015 in three durum wheat sub-populations; (B) LS means of Leth2012_AM and Leth2013_AM field data; (C) LS means of AUDPC calculated from 3 assessments (19-Aug, 27-Aug and 03-Sep-2013) in Toluca, Mexico 2013. Bars that do not share a letter differ significantly (Fisher's LSD, $P < 0.05$). Data are presented as mean ± standard error; (D) Square root transformation of AUDPC data for Mexico 2013.



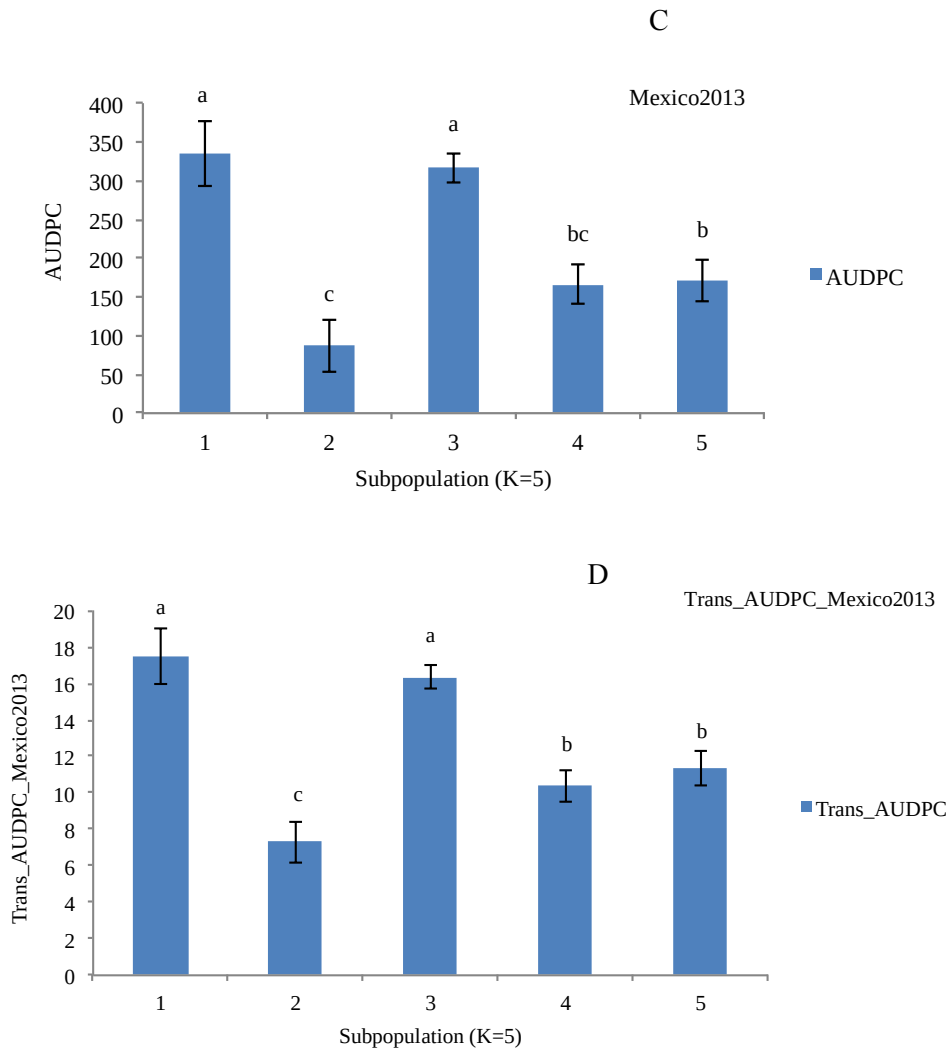


Figure 10. The second time point scorings in three durum wheat subpopulations inoculated with (A) MI, single isolate W009 and W015 in five durum wheat sub-populations; (B) LS means of Leth2012_AM and Leth2013_AM field data; (C) LS means of AUDPC calculated with 3 time ratings (19-Aug, 27-Aug and 03-Sep-2013) in Toluca, Mexico 2013. Bars that do not share a letter differ significantly (Fisher's LSD, $P < 0.05$). Data are presented as mean ± standard error; (D) Square root transformation of AUDPC data for Mexico 2013

For the field data Leth2012_AM, accessions in K=3_Pop3 had the highest severity (39.8 ± 2.8), while accessions in K=3_Pop1 (22.1 ± 3.1) and K=3_Pop2 (22.8 ± 4.2) expressed lower severity, but not significantly different from each other. The field data Leth2013_AM had the same distribution as Leth2012_AM, accessions in K=3_Pop3 expressed the highest severity (20.6 ± 1.6), while accessions in K=3_Pop1 (10.1 ± 1.8) and K=3_Pop2 (10.4 ± 2.4) were less severely infected and similar to each other (Figure 9B). For the AUDPC calculated using three time ratings (19-Aug, 27-Aug and 03-Sep-2013) in Toluca, Mexico 2013, accessions in K=3_Pop3

expressed the highest severity (326.7 ± 17.7), while accessions in K=3_Pop1 (149.4 ± 19.8) and K=3_Pop2 (141.6 ± 26.8) expressed significantly ($P < 0.05$) lower severity (Figure 9C). The square-root transformed AUDPC data Trans_AUDPC_Mexico2013 followed the same distribution as Mexico2013, the accessions in K=3_Pop3 expressed the highest severity (16.6 ± 0.6), significantly higher than K=3_Pop1 (9.6 ± 0.7) and K=3_Pop2 (10.8 ± 1.0) (Figure 9D).

In the case where the AM population was classified into five sub-populations, the seedling test using MI indicated that the Australian accessions, which belong to K=5_Pop1, expressed the highest average severity (7.8 ± 0.5), while accessions in K=5_Pop2 had the lowest (4.2 ± 0.4). The North American accessions, K=5_Pop3 (6.7 ± 0.3) and K=5_Pop4 (6.5 ± 0.3) presented intermediate severity and were significantly higher ($P < 0.05$) than K=5_Pop5 (5.9 ± 0.3). For the seedling test using isolate W009, the LSD test indicated for Scoring_2, there were significant differences among the five sub-populations (Figure 10A). K=5_Pop1 had the highest severity (6.7 ± 0.4), while K=5_Pop2 had the lowest severity (3.9 ± 0.3), K=5_Pop3 (5.1 ± 0.2) and K=5_Pop4 (5.2 ± 0.3) were intermediate in severity and were significantly higher ($P < 0.05$) than K=5_Pop5 (4.5 ± 0.3). For seedling resistance to isolate W015, the LSD test showed that there were significant ($P < 0.05$) differences among the five sub-populations for Scoring_2 (Figure 10A). K=5_Pop1 (5.2 ± 0.4) and K=5_Pop3 (5.1 ± 0.3) showed the highest average severity, while K=5_Pop2 (3.5 ± 0.3) presented the lowest severity, and K=5_Pop4 (4.4 ± 0.3) and K=5_Pop5 (4.2 ± 0.3) presented an intermediate rating.

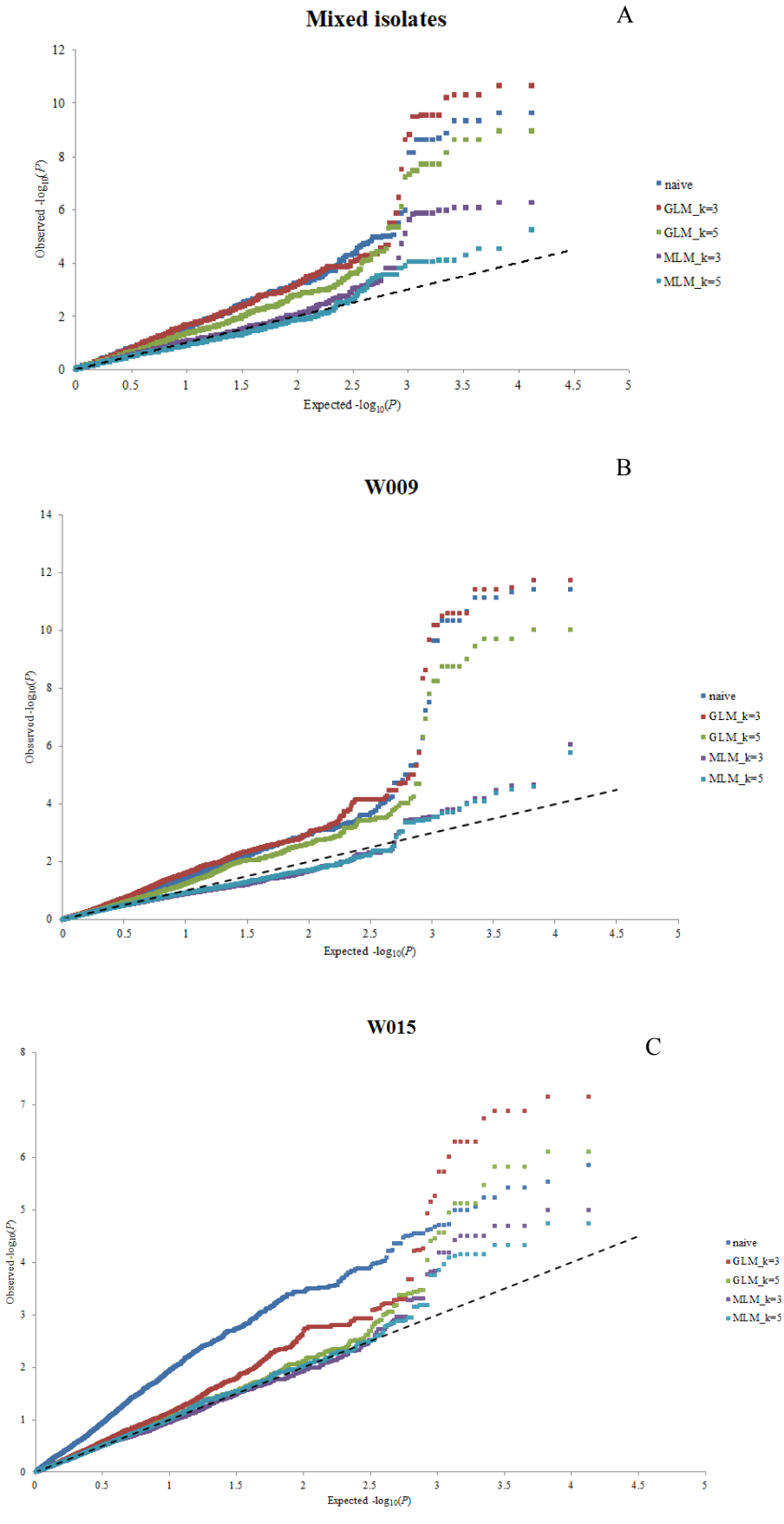
For the field data Leth2012_AM, only K=5_Pop3 (36.7 ± 3.3) and K=5_Pop4 (22.9 ± 4.2) differed significantly (Figure 10B). For the field data Leth2013_AM, there were significant differences among the five sub-populations (Figure 10B). K=5_Pop1 had the highest rating (21.7 ± 3.9), while K=5_Pop2 had the lowest rating (6.1 ± 3.0), K=5_Pop3 (19.8 ± 1.7) and K=5_Pop4 (10.2 ± 2.2) presented intermediate disease severity and was not significantly different than K=5_Pop5 (13.8 ± 2.5).

For the AUDPC value from Mexico 2013, there were significant differences among the five sub-populations (Figure 10C). K=5_Pop1 had the highest AUDPC value (335.1 ± 43.1), while K=5_Pop2 had the lowest value (86.3 ± 32.9), K=5_Pop3

(316.9 ± 19.3) had intermediate AUDPC value and was significantly higher than K=5_Pop4 (165.8 ± 24.9) and K=5_Pop5 (171.6 ± 27.7). The square-root transformed AUDPC data Trans_AUDPC_Mexico2013 followed the same distribution as Mexico2013, K=5_Pop1 had the highest AUDPC value (17.5 ± 1.5), while K=5_Pop2 had the lowest value (7.3 ± 1.2), K=5_Pop3 (16.4 ± 0.7) had intermediate AUDPC value and was significantly higher than K=5_Pop4 (10.4 ± 0.9) and K=5_Pop5 (11.3 ± 1.0).

5.1.4 Marker-trait association

In the Q-Q plot, the observed distribution of association analysis statistics (Y-axis) was plotted against expected values (X-axis). Any markers with a *P*-value deviating from the Y=X line indicated genome-wide differences from the control. Association analysis of seedling resistance to MI was conducted with three different models: the naïve model without Q or K matrix, the general linear model (GLM) with Q matrix only, and the mixed linear model with both Q and K matrix. For seedling resistance to the MI, single isolate W009 and W015, and adult plant resistance Trans_AUDPC_Mexico2013, the quantile-quantile (Q-Q) plot (Figures 11A, B, C, and F) illustrated that the naïve model and GLM showed confounding/bias because of uncontrolled population structure or kinship relationship. The MLM showed a clean line matching Y = X, except for the upturn at the end, which indicated a few associated markers among thousands of un-associated markers. Therefore, MLM was adopted for the association mapping. For adult plant resistance Leth2012, Figure 11D illustrated that the naïve model was confounded/biased while no significant markers were detected using either GLM or MLM. For adult plant resistance Leth2013, Figure 11E illustrated that naïve and GLM models were confounded/biased, while no significant markers were detected using MLM.


Mixed isolates
A
Observed -log10(P)
Expected -log10(P)
naive
GLM_k=3
GLM_k=5
MLM_k=3
MLM_k=5
B
W009
Observed -log10(P)
Expected -log10(P)
naive
GLM_k=3
GLM_k=5
MLM_k=3
MLM_k=5
W015
C
Observed -log10(P)
Expected -log10(P)
naive
GLM_k=3
GLM_k=5
MLM_k=3
MLM_k=5

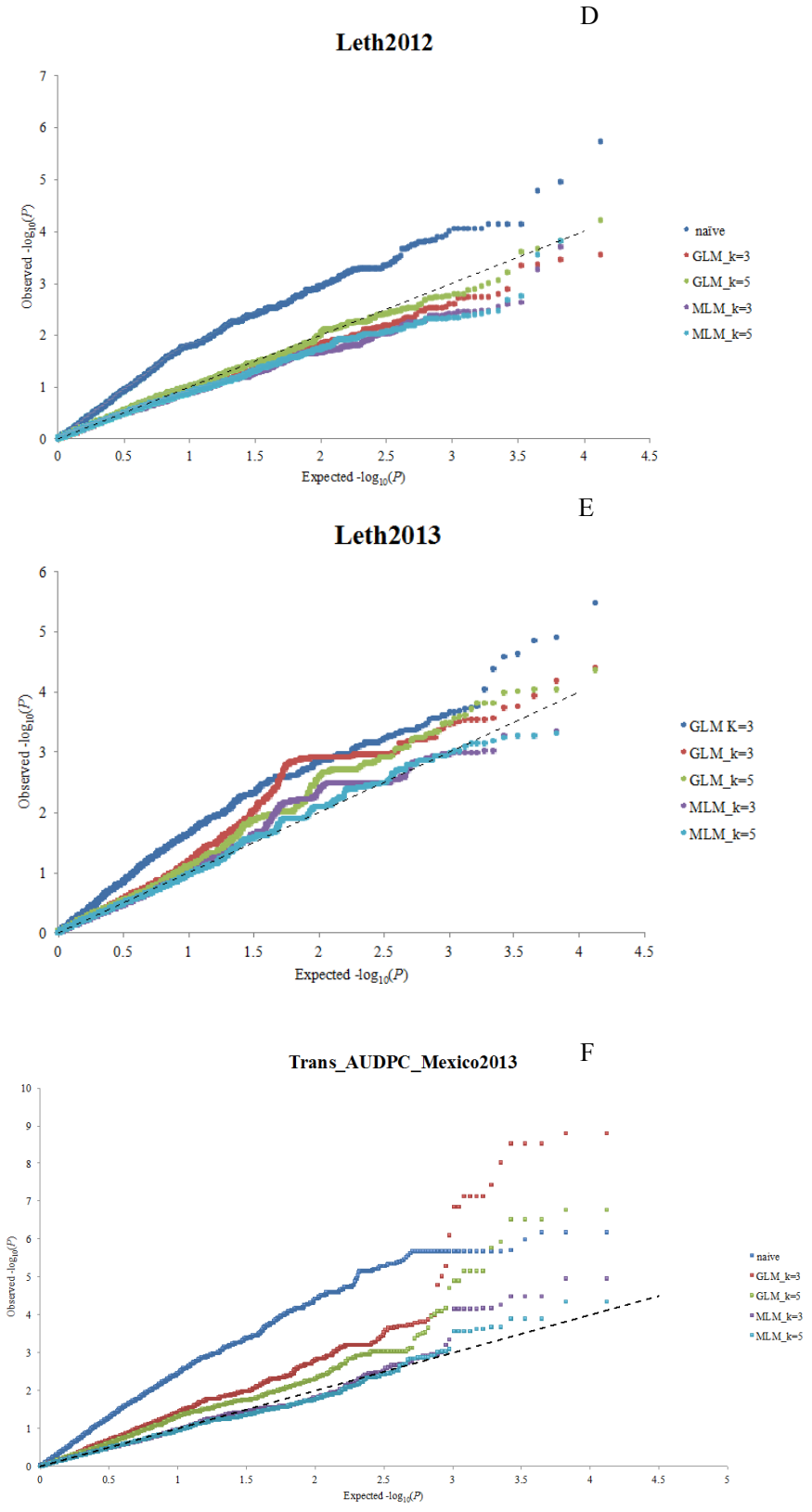


Figure 11. Quantile–Quantile (Q-Q) plot of five different models: naïve model, GLM (with 3 or 5 sub-populations) and MLM (with 3 or 5 sub-populations). The Q-Q plot was based on the seedling test of (A) MI, (B) isolate W009, (C) isolate W015, and (D) adult plant resistance for Leth2012_AM, (E) Leth2013_AM and (F) AUDPC calculated using adult plant resistance in Mexico 2013.

The results of marker-trait association analysis are summarized in Figure 12 where SNP-trait associations were discovered using MLM.

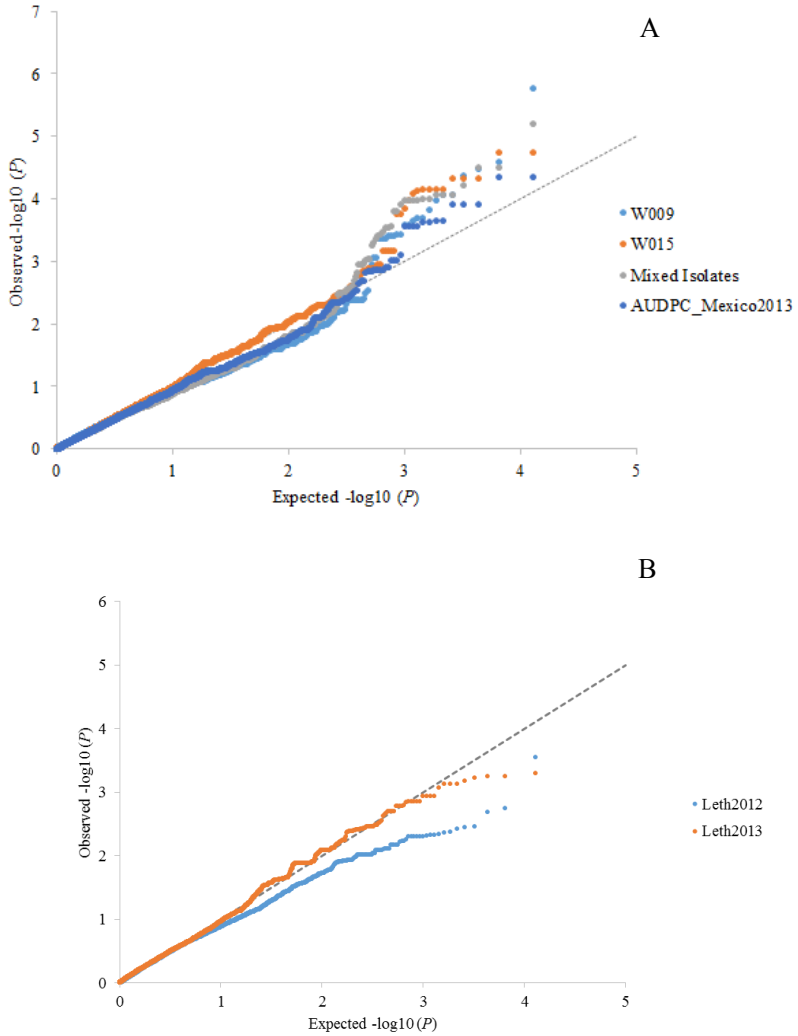


Figure 12. Quantile–Quantile (Q-Q) plot of MLM define for (A) AUDPC data collected from Mexico 2013 using MI, single isolate W009 and W015. The expected *P*-values were plotted against observed *P*-values for each SNP, the diagonal line represented the null hypothesis no association. (B) Q-Q plot of MLM for Leth2012_AM and Leth2013_AM field data.

The Q-Q plot for the seedling test using MI (Figure 12A) shows, that the distribution of observed *P*-values had a small digression from the diagonal line, except for extremely low *P*-values, which represented 15 significantly associated SNPs. All 15 SNPs and 1 SSR marker were determined to be significant (permutation $P < 0.05$) using MLM, and were located at the same location on chromosome 7BL (Table 17). This indicated one potential QTL site related to seedling stripe rust

resistance in this AM panel. Two additional markers on chromosome 7BL, CAP7_c3950_160 (228.2 cM) and Tdurum_contig49656_789 (222.5 cM), were detected when the AM population was divided into three sub-populations. Thus, an identical chromosome region on chromosome 7BL was detected, regardless if three or five sub-populations were used for the analysis. These 15 markers were also significant (FDR $Q < 0.05$) with the MLM_K=3 model using the FDR multiple test correction (Table 18); no significant markers could be detected with MLM_K=5.

Table 17. Summary of chromosome 7BL markers significantly associated with stripe rust resistance in the AM population when evaluated by seedling reaction to MI, single isolates Yr09spi and Yr15spi and adult plant resistance reaction in Mexico 2013. Percentage of phenotypic variance explained (R^2) and effect of associated alleles. The bold SNP allele had effects indicated in the Effect column. The locations of the markers were determined by the consensus map of Maccaferri, et al. (2014). Non-significant markers were indicated by not significant (NS).

SNP / SSR ID	Chr.	Position (cM)	SNP / SSR	MI			W009			W015			Trans AUDPC Mexico (2013)		
				P-value	R^2 (%) [b]	Effect [c]	*P*-value	R^2 (%) [b]	Effect [c]	*P*-value	R^2 (%) [b]	Effect [c]	*P*-value	R^2 (%) [b]	Effect [c]
Excalibur_c51720_84	7B	187.5	A/**C**	0.0003	21.3	-1.44	0.001	24.3	-1.18	0.022	17.1	-1.17	0.02	15.8	-4.97
RAC875_c54854_164	n/a	n/a	G/**A**	0.0005	22.8	-1.96	0.001	31.1	-2.18	NS			0.006	17.1	-5.35
BS00022162_51	7B	187.5	A/**G**	0.0003	21.3	-1.44	0.001	24.3	-1.18	0.022	17.1	-1.17	0.02	15.8	-4.97
Tdurum_contig61884_836	7B	186.0	A/**G**	0.0001	23.1	0.71	NS			NS			NS		
Tdurum_contig49575_1237	7B	187.5	A/**G**	0.0001	25.2	-1.54	0.001	29.7	-1.27	0.001	20.4	-1.26	0.001	20.4	-5.62
Kukri_c46447_1738	7B	187.5	G/**A**	0.0003	21.3	-1.44	0.001	24.3	-1.18	0.022	17.1	-1.17	0.02	15.8	-4.97
Kukri_c3781_285	7B	187.5	A/**G**	0.0001	25.2	-0.77	0.001	29.7	-0.64	0.001	20.4	-0.63	0.001	20.4	-2.81
BobWhite_c12355_1590	n/a	n/a	G/**A**	0.0004	23.2	-1.46	0.001	24.3	-1.18	NS			0.038	16.2	-5.06
Tdurum_contig42586_720	7B	187.5	G/**A**	0.0001	24.1	-0.74	0.001	27.7	-0.60	0.005	19.2	-0.60	0.001	19.4	-2.64
Excalibur_c1070_2327	7B	187.5	G/**A**	0.0003	21.3	-1.44	0.001	24.3	-1.18	0.022	17.1	-1.17	0.02	15.8	-4.97
Tdurum_contig42586_290	7B	187.5	C/**A**	0.0001	24.1	-0.74	0.001	27.7	-0.60	0.005	19.2	-0.60	0.001	19.4	-2.64
Tdurum_contig42586_990	7B	187.5	A/**G**	0.0001	24.1	-0.74	0.001	27.7	-1.20	0.005	19.2	-0.60	0.001	19.4	-2.64
RAC875_rep_c111788_253	7B	186.0	A/**G**	0.0003	24.8	1.50	NS			0.02	17.8	1.23	NS		
Tdurum_contig49575_1207	7B	187.5	G/**A**	0.0004	23.2	-1.46	0.001	24.3	-1.18	NS			0.038	16.2	-5.06
Kukri_c48418_149	7B	187.5	A/**C**	0.0001	25.5	-0.66	0.001	32.3	-1.10	0.011	21.1	-0.20	0.005	20.5	-0.50
cfa2040	7B	184.5	n/a	0.000003	26.9	-0.92 ~0.92	NS			NS			NS		

Table 18. Significant marker-phenotype associations (FDR *Q* value < 0.05) after multiple test correction using the FDR method, no significant markers were detected using MLMs of Trans AUDPC Mexico (2013), MLM_K=5 of MI, or MLM_K=5 of W015, indicated by NS.

Markers	**MI_MLM_K=3**	**W009_MLM_K=3**	**W009_MLM_K=5**	**W015_MLM_K=3**
		Q value		
Kukri_c3781_285	0.002	NS	NS	0.046
Tdurum_contig49575_1237	0.002	NS	NS	0.046
Tdurum_contig42586_290	0.002	NS	NS	0.046
Tdurum_contig42586_720	0.002	NS	NS	0.046
Tdurum_contig42586_990	0.002	NS	NS	0.046
BobWhite_c12355_1590	0.002	NS	NS	NS
Tdurum_contig49575_1207	0.002	NS	NS	NS
BS00022162_51	0.002	NS	NS	0.046
Excalibur_c1070_2327	0.002	NS	NS	0.046
Excalibur_c51720_84	0.002	NS	NS	0.046
Kukri_c46447_1738	0.002	NS	NS	0.046
RAC875_c54854_164	0.002	0.011	0.021	NS
Kukri_c48418_149	0.002	NS	NS	NS
RAC875_rep_c111788_253	0.008	NS	NS	NS
Tdurum_contig61884_836	0.017	NS	NS	NS

[a] Non-significant markers after correction using FDR method.

The pattern of the Q-Q plot for the single isolates W009 and W015 tested at the seedling stage, was similar to that of the MI (Figure 12A). There were 13 markers for W009 and 11 markers for W015 detected (permutation $P < 0.05$). The markers identified were the same as the 15 SNPs detected using the MI (Table 17). When the AM population was divided into three sub-populations, three more markers were detected using W009 and W015, they were: Tdurum_contig61884_836, Tdurum_contig49656_789 and RAC875_rep_c111788_253 for W009; and Tdurum_contig61884_836, BobWhite_c12355_1590 and Tdurum_contig49575_1207 for W015. All were located at 222.5 cM on chromosome 7BL. Using the FDR multiple test correction to analyze data of W015, only one marker was significant (FDR $Q < 0.05$) with MLM_K=3 and MLM_K=5, and for W015 9 markers were significant with MLM_K=3 (Table 18).

There were 13 SNP markers (permutation $P < 0.05$) detected using the transformed data AUDPC data from Mexico 2013 (Figure 12A, Table 17). They were located at the same position as the 15 significant SNPs detected using the MI. Taken together, these results indicate that the same QTL regions were detected using MI, isolates W009 and W015, and the transformed field data AUDPC data from Mexico 2013. Two more markers, CAP7_c3950_160 and RAC875_rep_c111788_253, were detected when we divided the AM population into three sub-populations, located at 228.2 cM and 222.5 cM on chromosome 7BL, respectively. However, these 13 significant markers were no longer significant using the permutation test after correction by the FDR method (Table 18). There were no significant markers detected using the field data Leth2012_AM and Leth2013_AM because of the deflation of *P*-value (Figure 12B).

The 92 accessions in the AM panel were assigned to 12 haplotypes (Table 19). Five major haplotypes (H2, H4, H5, H10, and H12) contained 85 accessions and the other 7 haplotypes contained a single accession. For seedling resistance data Scoring_2_MI, accessions in haplotype H2 and H12 were more severely diseased than those in haplotype H4 and H5 ($P < 0.01$), while H12 accessions were also more susceptible than H10 accessions ($P < 0.05$). The fact that the 92 elite cultivars were divided among multiple haplotypes, suggested that this QTL region was not strongly selected in the breeding programs.

Table 19. Haplotypes identified in the AM panel using 15 SNPs (permutation $P < 0.05$) associated with stripe rust resistance.

Haplotype	Num. of accessions	Average of Scoring_2_MI)	BobWhite_c12355_1590 Tdurum_contig49575_1207	Excalibur_c1070_2327 Kukri_c46447_1738	RAC875_rep_c111788_253	BS00022162_51	Kukri_c3781_285	Tdurum_contig42586_990	Excalibur_c51720_84	Kukri_c48418_149	RAC875_c54854_164	Tdurum_contig42586_290	Tdurum_contig42586_720	Tdurum_contig61884_836	Tdurum_contig49575_1237
H1	1	7.0	AG	AG	AG	AG	AA	AA	AC	AA	--	CC	GG	GG	AA
H2	10	6.1	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
H3	1	1.6	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
H4	35	4.1	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
H5	8	4.1	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
H6	1	6.3	AA	AA	AA	GG	GG	GG	CC	AC	AG	AA	AA	AA	AG
H7	1	8.4	AA	AA	--	GG	AA	--	CC	CC	AA	--	--	--	AA
H8	1	5.4	AA	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
H9	1	4.9	AG	AG	AG	AG	AA	AA	AC	CC	--	CC	GG	GG	AA
H10	6	4.9	AG	AG	AG	AG	AA	AA	AC	CC	AA	CC	GG	GG	AA
H11	1	5.5	AG	AG	AA	AG	AA	AA	AC	CC	AG	CC	GG	AA	AA
H12	26	6.2	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA

5.2 Genetic mapping of stripe rust resistance in a DH population

5.2.1 Phenotypic data

In the double haploid (DH) population Kofa x W9262-260D3, seedling tests were conducted in phytotron experiments using single isolates W009 (Figure 13) and W015. In the ANOVA test for seedling resistance to single isolates W009 and W015, there were effects of blocks nested within replicates and significant differences ($P < 0.001$) among accessions for both Scoring_1 and Scoring_2 (Table 20).

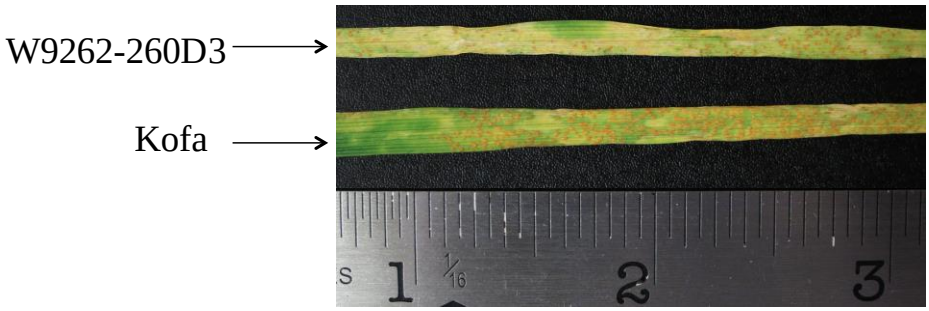


Figure 13. Parental reactions to stripe rust isolate W009.

Table 20. Variance estimates for random effects and F-values for fixed effect from ANOVA of two assessments (Scoring_1 and Scoring_2) of DH population seedling reaction to a single isolates W009 and W015.

Effect	Seedling resistance to stripe rust			
	W009		W015	
	Scoring_1	**Scoring_2**	**Scoring_1**	**Scoring_2**
RANDOM EFFECTS VARIANCE ESTIMATES				
Rep	0.749	0.177	0.185	0.0992
Block (Rep)	0.393***	0.0706*	0.372***	0.295***
Residual	0.830***	0.559***	0.835***	0.696***
FIXED EFFECT F-VALUES				
Accession	9.430***	16.620***	5.350***	6.680***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

The phenotypic data was quantitatively expressed, however, dividing accessions into resistance and susceptibility based on a disease severity score of less than 4 and equal or bigger than 4, the ratio between resistant and susceptible individuals was 20.6% vs. 73.5% for isolate W009 and 21.3% vs. 78.7% for isolate W015 (Figures 14A and B). Both ratios were not significantly different from a 1:3 ratio (Table 21, Chi-square test; $P > 0.05$), which suggests that two unlinked genes condition

resistance in this population.

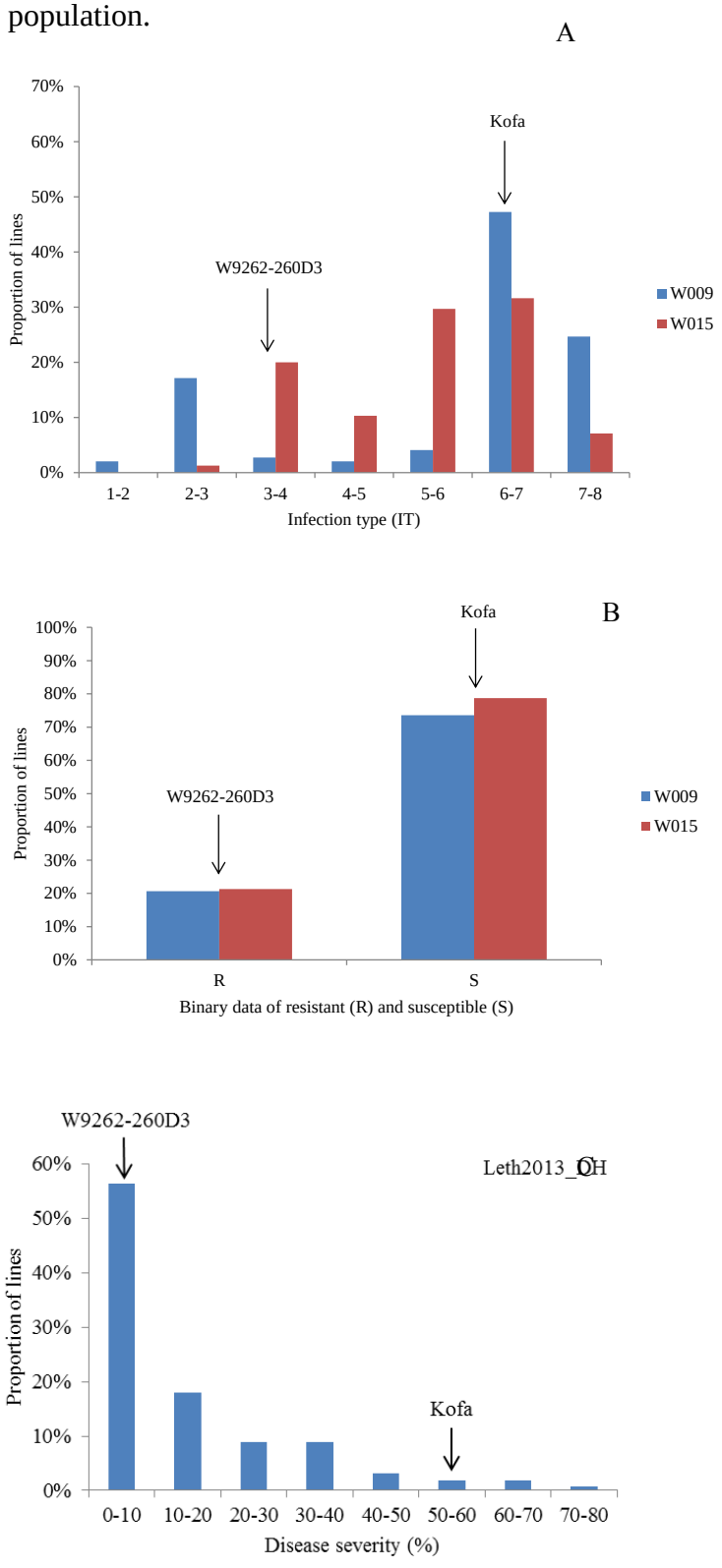


Figure 14. Frequency distributions for DH population (Kofa x W9262-260D3): (A) seedling disease reaction to single isolates W009 and W015, (B) frequency distribution of binary transformed disease resistance to single isolate W009 and W015, and (C) field data Leth2013_DH. The individuals with IT ratings 0-4 and 4-9 were scored as R and S, respectively.

Table 21. Chi-square test of reaction of DH population from the cross of Kofa/W9262-260D3.

Parents	Isolate	Number of DH lines [a]		Expected ratio [b]	χ^2	*P*-value
		R	S			
Kofa/W9262-260D3	W009	32	114	1:3	0.740	0.390
	W015	33	122	1:3	1.138	0.286

[a] Number of DH lines with resistant (R) or susceptible (S) reactions to stripe rust single isolates

[b] Ratio of resistant to susceptible lines

In contrast to greenhouse seedling tests, field evaluation at the adult plant stage indicated that disease severity of the DH population in the field (Leth2013_DH) was low (Figure 14C).

The DH population showed transgressive segregation for seedling and adult plant resistance to stripe rust. For seedling resistance to W009, 18.7% of the DH population had a higher level of resistance than W9262-260D3 (resistant parent), while 23.2% were more susceptible than Kofa (susceptible parent). For seedling resistance to W015, 12.3% of the DH population were more resistant than W9262-260D3, while 35.5% were more susceptible than Kofa. For adult plant resistance in Lethbridge 2013, 43.9% of the DH population were more resistant than W9262-260D3, whereas 1.9% were more susceptible than Kofa.

5.2.2 QTL map construction and QTL identification

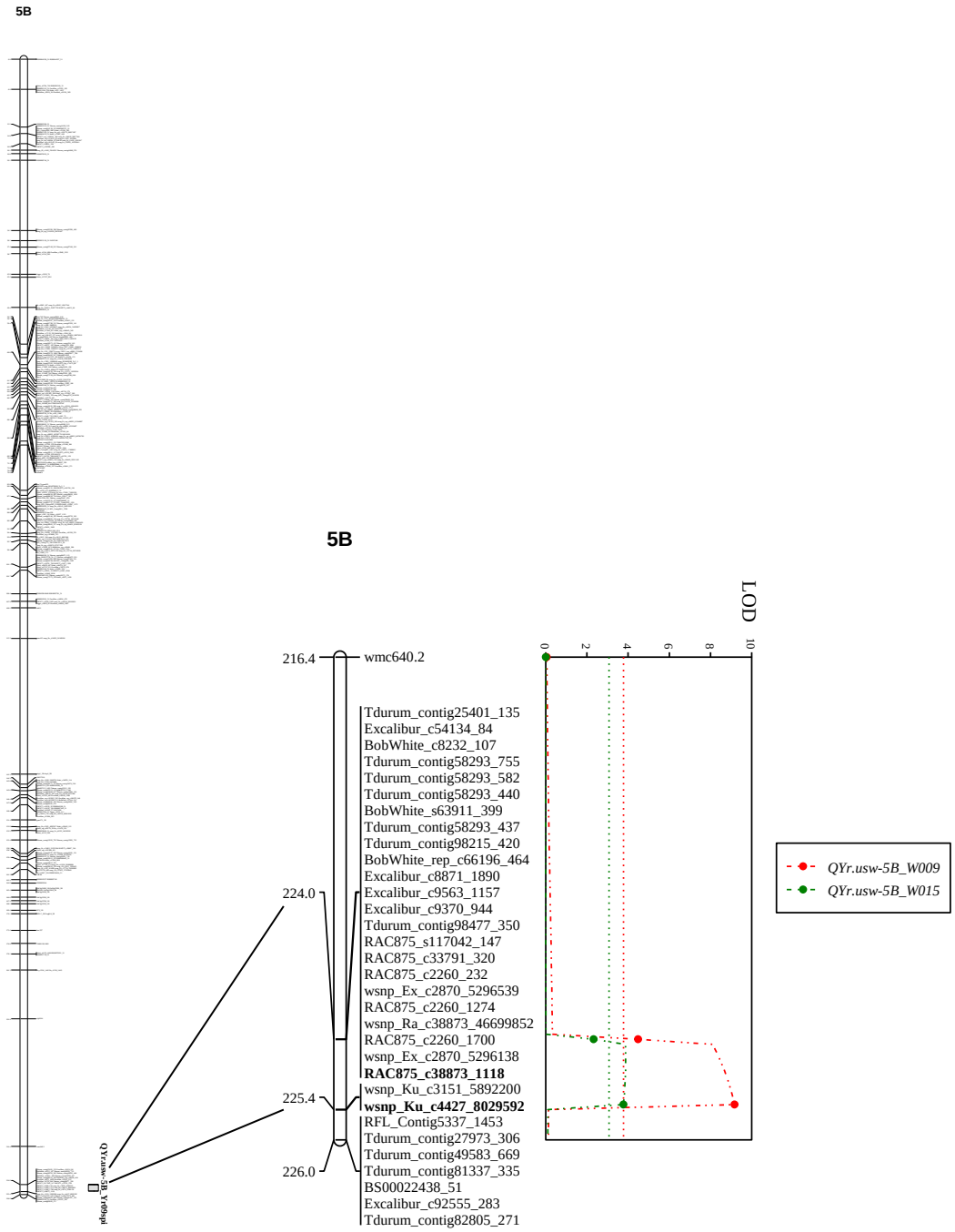
A genetic map for this population existed (N'Daiye, unpublished data), and consists of 10,768 SNPs and 107 SSR markers. The genetic map covers 2,639.7 cM with an average interval size of 0.64 markers/cM, containing 13 linkage gaps larger than 10 cM on 1A, 1B, 3A, 3B, 4A, 5A and 6A (Table 22). This genetic map was used in part to construct the recent high density consensus map of durum wheat (Macafferi et al. 2014).

Table 22. Mapping statistics for the genetic map consisting 10,875 markers of DH population (N'Daiye, unpublished data).

Chromosome	Length (cM)	Num. of markers unique mapped	Density (Num. of markers/cM)	Max. gap (cM)	Num. of gaps larger than 10 cM
1A	126.6	41	0.32	22.87	4
1B	214.6	168	0.78	14.06	1
2A	151.4	108	0.71	8.85	0
2B	199.7	179	0.90	9.57	0
3A	143.0	61	0.43	24.96	4
3B	220.0	126	0.57	20.64	1
4A	164.1	91	0.55	13.48	1
4B	141.9	87	0.61	6.90	0
5A	195.5	94	0.48	14.75	1
5B	246.3	181	0.73	7.08	0
6A	156.2	100	0.64	10.88	1
6B	201.4	145	0.72	8.33	0
7A	207.7	126	0.61	7.99	0
7B	271.3	181	0.67	7.58	0
Whole genome	2639.7	1688	0.64	24.96	13

For isolate W009, the threshold LOD scores were 3.22 and 3.78 for CIM, at the significance levels of $P < 0.05$ and $P < 0.01$, respectively. There were two QTLs above the permutation thresholds (permutation $P < 0.01$). The QTL with largest effect, *QYr.usw-7B_W009*, was located on chromosome 7BL. It was flanked by markers *BS00003929* - *BS00075300_51* and had a LOD scores of 6.95 to 11.47 and explained 19.7 - 30.4% of the phenotypic variance (R^2). Another major QTL, *QYr.usw-5B*, located on chromosome 5BL, was flanked by markers *RAC875_c38873_1118* - *wsnp_Ku_c4427_8029592*. It had LOD scores of 4.49 to 9.17 and explained 13.2 - 25.1% of phenotypic variance (R^2) (Figure 15, Table 23). For isolate W015, the threshold LOD scores were 3.07 and 3.94 for CIM, at significant levels of $P < 0.05$ and $P < 0.01$, respectively. Based on the QTL analysis, there were two QTLs above the permutation thresholds (permutation $P < 0.05$). The QTL with largest effect, *QYr.usw-7B_W015*, was located on chromosome 7BL. It was flanked by markers *BS00075300_51* - *BobWhite_c2892_211* and had LOD scores of 6.87 to 8.59 and explained 18.6 - 22.7% of phenotypic variation (R^2). Another major QTL, *QYr.usw-5B*, located on chromosome 5BL, flanked by markers *RAC875_c38873_1118* and *wsnp_Ku_c4427_8029592*. It had LOD scores of 3.77 to 3.88 and explained 10.7 – 11.0% of phenotypic variance (R^2) (Table 24).

(A)


5B
5B
LOD
0
2
4
6
8
10
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224.0
225.4
226.0
wmc640.2
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Excalibur_c54134_84
BobWhite_c8232_107
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Tdurum_contig58293_437
Tdurum_contig98215_420
BobWhite_rep_c66196_464
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Excalibur_c9563_1157
Excalibur_c9370_944
Tdurum_contig98477_350
RAC875_s117042_147
RAC875_c33791_320
RAC875_c2260_232
wsnp_Ex_c2870_5296539
RAC875_c2260_1274
wsnp_Ra_c38873_46699852
RAC875_c2260_1700
wsnp_Ex_c2870_5296138
RAC875_c38873_1118
wsnp_Ku_c3151_5892200
wsnp_Ku_c4427_8029592
RFL_Contig5337_1453
Tdurum_contig27973_306
Tdurum_contig49583_669
Tdurum_contig81337_335
BS00022438_51
Excalibur_c92555_283
Tdurum_contig82805_271
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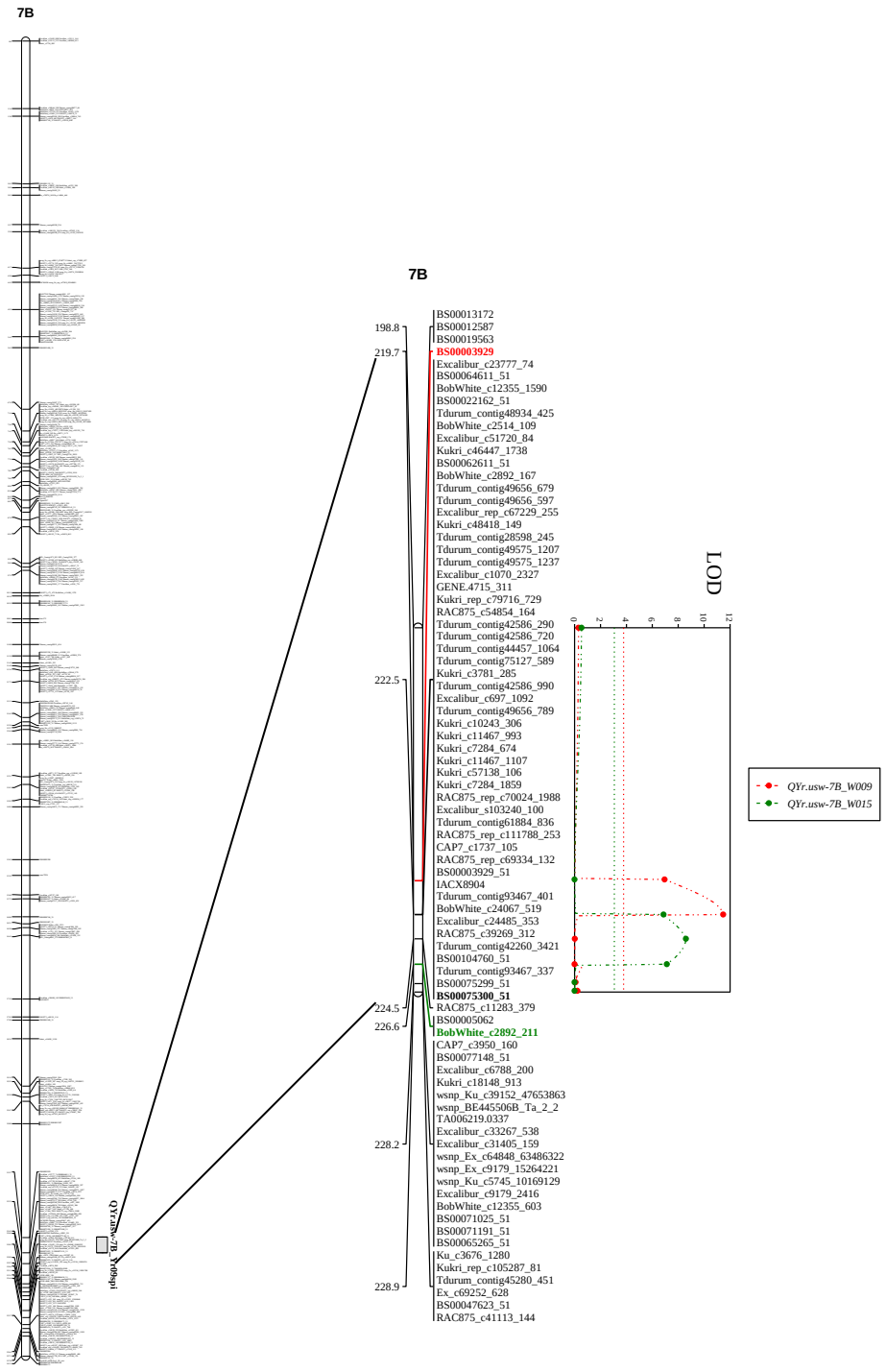
QYr.usw-5B_W009
QYr.usw-5B_W015

(B)


7B
7B
198.8
219.7
222.5
224.5
226.6
228.2
228.9
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BS00013172
BS00012587
BS00019563
BS00003929
Excalibur_c23777_74
BS00064611_51
BobWhite_c12355_1590
BS00022162_51
Tdurum_contig48934_425
BobWhite_c2514_109
Excalibur_c51720_84
Kukri_c46447_1738
BS00062611_51
BobWhite_c2892_167
Tdurum_contig49656_679
Tdurum_contig49656_597
Excalibur_rep_c67229_255
Kukri_c48418_149
Tdurum_contig28598_245
Tdurum_contig49575_1207
Tdurum_contig49575_1237
Excalibur_c1070_2327
GENE.4715_311
Kukri_rep_c79716_729
RAC875_c54854_164
Tdurum_contig42586_290
Tdurum_contig42586_720
Tdurum_contig44457_1064
Tdurum_contig75127_589
Kukri_c3781_285
Tdurum_contig42586_990
Excalibur_c697_1092
Tdurum_contig49656_789
Kukri_c10243_306
Kukri_c11467_993
Kukri_c7284_674
Kukri_c11467_1107
Kukri_c57138_106
Kukri_c7284_1859
RAC875_rep_c70024_1988
Excalibur_s103240_100
Tdurum_contig61884_836
RAC875_rep_c111788_253
CAP7_c1737_105
RAC875_rep_c69334_132
BS00003929_51
IACX8904
Tdurum_contig93467_401
BobWhite_c24067_519
Excalibur_c24485_353
RAC875_c39269_312
Tdurum_contig42260_3421
BS00104760_51
Tdurum_contig93467_337
BS00075299_51
BS00075300_51
RAC875_c11283_379
BS00005062
BobWhite_c2892_211
CAP7_c3950_160
BS00077148_51
Excalibur_c6788_200
Kukri_c18148_913
wsnp_Ku_c39152_47653863
wsnp_BE445506B_Ta_2_2
TA006219.0337
Excalibur_c33267_538
Excalibur_c31405_159
wsnp_Ex_c64848_63486322
wsnp_Ex_c9179_15264221
wsnp_Ku_c5745_10169129
Excalibur_c9179_2416
BobWhite_c12355_603
BS00071025_51
BS00071191_51
BS00065265_51
Ku_c3676_1280
Kukri_rep_c105287_81
Tdurum_contig45280_451
Ex_c69252_628
BS00047623_51
RAC875_c41113_144
LOD
0
2
4
6
8
10
12
QYr.usw-7B_W009
QYr.usw-7B_W015

Figure 15. Mapping of QTLs for seedling stripe rust resistance in the Kofa/W9262-260D3 DH population. The QTL map was constructed using 10,768 SNP and 107 SSR markers. The position of two significant QTLs on chromosome 5BL (A) and 7BL (B) are illustrated by diagonally hatch bars next to the chromosome. Flanking markers of *QYr.usw-7B_W009* and *QYr.usw-7B_W015* were indicated in red and green, respectively, and common markers were indicated in black bold.

Table 23. QTLs for seedling stripe rust resistance to single isolate W009 identified using the Kofa/W9262-260D3 DH population (permutation $P < 0.01$).

QTL	Chr.	Flanking markers	Peak marker	LOD	R^2 (%)	Additive effect
QYr.usw-5B	5BL	RAC875_c38873_1118 - wsnp_Ku_c4427_8029592	wsnp_Ku_c4427_8029592	4.49 - 9.17	13.2 - 25.1	0.79
QYr.usw-7B_W009	7BL	BS00003929 - BS00075300_51	BS00075300_51	6.95 - 11.47	19.7 - 30.4	0.90

Table 24. QTLs for seedling stripe rust resistance to single isolate W015 identified using the Kofa/W9262-260D3 DH population (permutation $P < 0.05$).

QTL	Chr.	Flanking markers	Peak marker	LOD	R^2 (%)	Additive effect
QYr.usw-5B	5BL	RAC875_c38873_1118 - wsnp_Ku_c4427_8029592	wsnp_Ku_c4427_8029592	3.77 - 3.88	10.7 - 11.0	0.35
QYr.usw-7B_W015	7BL	BS00075300_51 - BobWhite_c2892_211	RAC875_c11283_379	6.87 - 8.59	18.6 - 22.7	0.55

In the meta-analysis using Biomercator software, QTLs identified in independent experiments were treated as single QTL based on the Akaike-information criterion (AIC) value. The smaller the AIC value was, the better the model was when comparing the two models. In this study, the model that aggregated meta-QTL was smaller (AIC value = 7.60) than that at two QTLs (AIC = 9.59). The meta-QTL *QYr.usw-7B* was located at 223.2 cM of chromosome 7BL, with a 95% confidence interval (CI) of 0.36 cM (Figure 16).

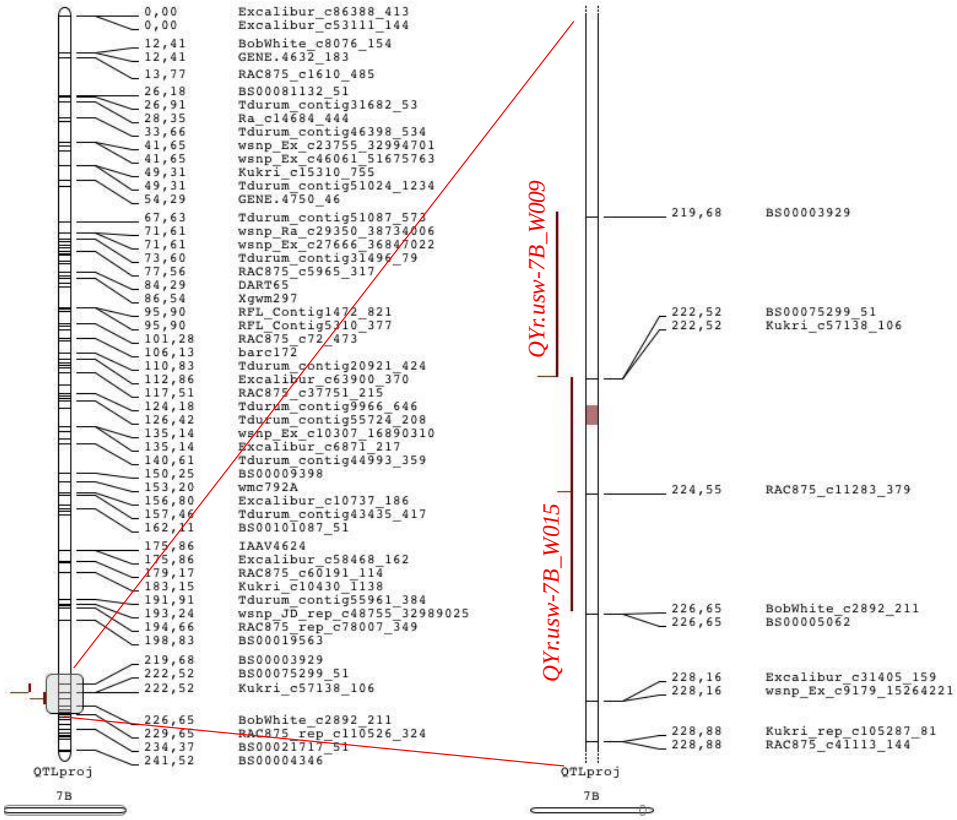


Figure 16. QTL meta-analysis aggregated the adjacent QTLs, *QYr.usw-7B_W009* and *QYr.usw-7B_W015*. These two QTLs were illustrated by vertical lines, the red stripe on the chromosome represents the meta-QTL located from 223.0 cM to 223.4 cM, with a peak LOD value at 223.2 cM on chromosome 7BL.

For the field data from Lethbridge collected in 2013, the threshold permutation LOD scores were 3.02 and 3.58 for CIM, at the significance levels of $P < 0.05$ and $P < 0.01$, respectively. Three QTL regions were detected at significance level of $P < 0.05$, located on chromosome 2B, 5A and 5B (Table 25, Figure 17). The positions of these three QTLs were different from QTLs detected using seedling resistance data.

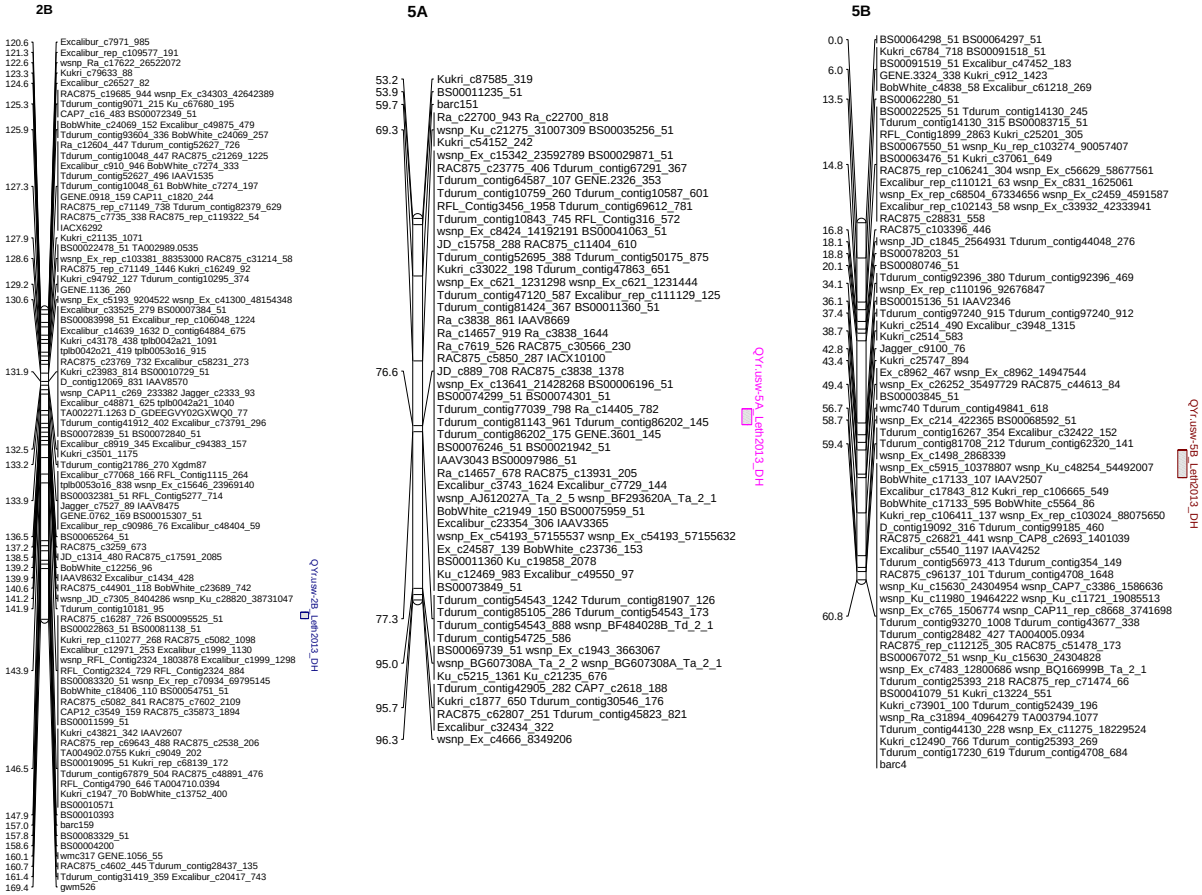


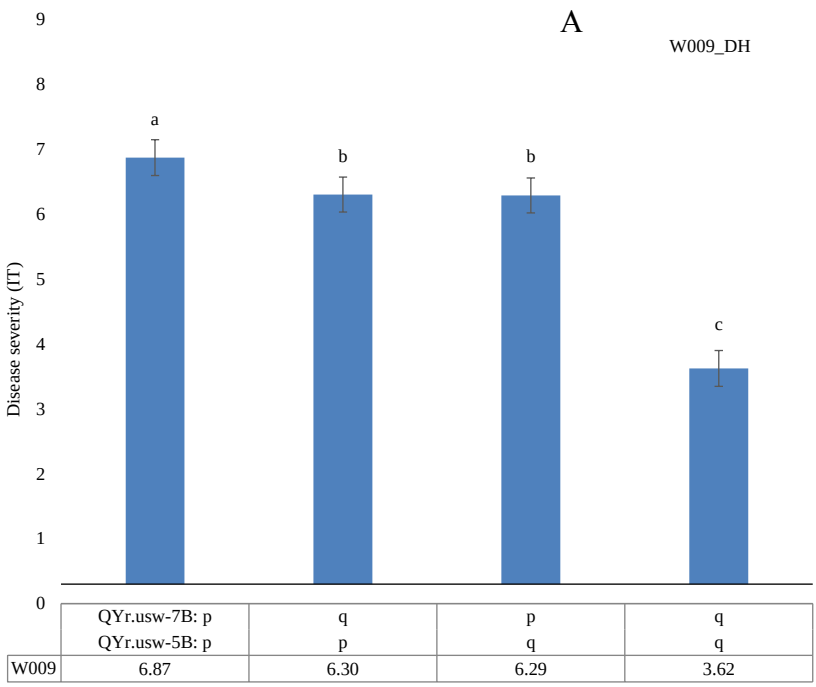
Figure 17. The QTLs for adult plant resistance detected using the Kofa/W9262-260D3 DH population, using the field data from Lethbridge collected in 2013. The position of three significant QTLs on chromosome 2B, 5A and 5B were illustrated by blue, pink and brown bars next to the chromosomes, respectively.

Table 25. QTLs for adult plant resistance data from Leth 2013_DH identified using the Kofa/W9262-260D3 DH population (permutation $P < 0.05$).

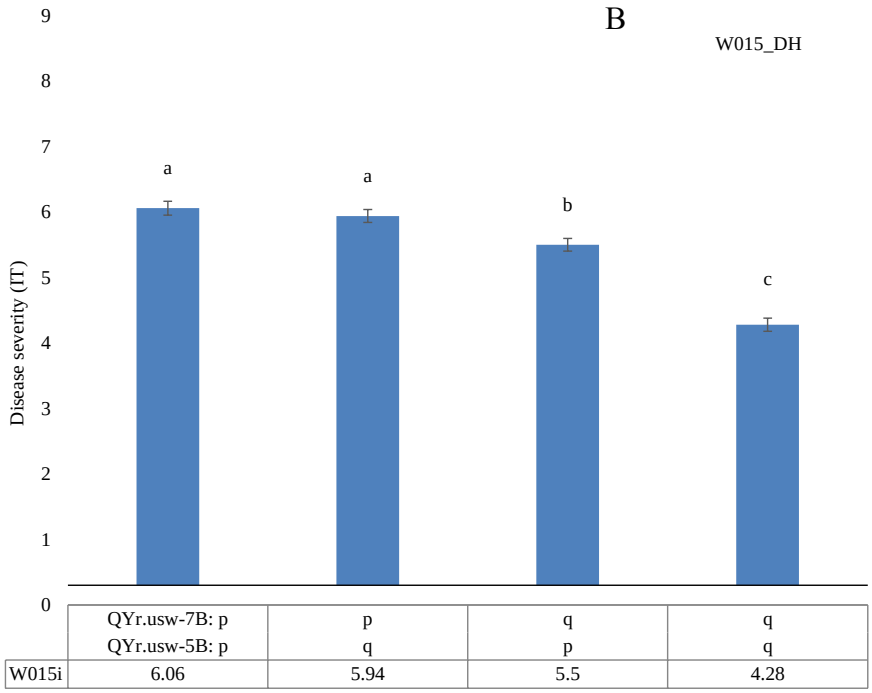
QTL	Chr.	Flanking markers	Peak marker	LOD	R^2 (%) [a]	Add-effect [b]
QYr.usw-2B_Leth2013_DH	2B	gwm526	gwm526	3.24	9.2	-3.99
QYr.usw-5A_Leth2013_DH	5A	BS00073849_51	BS00073849_51	3.32	9.4	3.94
QYr.usw-5B_Leth2013_DH	5B	Kukri_c2514_583 - Kukri_c25747_894	Jagger_c9100_76	4.63	12.9	4.68

5.2.3 QTL interaction

For seedling stripe rust resistance to single isolates W009 and W015, there was significant epistatic interaction ($P < 0.01$), which explained 12.7% and 17.1% of the phenotypic variance (Figures 18A and B), respectively. The results fit the expected 3 susceptible to 1 resistant segregation ratio consistent with the 3:1 ratio observed when the data were classified into qualitative groups (Tables 20 and 21). Taken together, the results of the Mendelian analysis and the QTL analysis support two independent resistance genes, one on chromosome 5B and the other on 7B that are both required for full expression of resistance in this population.



	QYr.usw-7B: p	q	p	q
	QYr.usw-5B: p	p	q	q
W009	6.87	6.30	6.29	3.62



	QYr.usw-7B: p	p	q	q
	QYr.usw-5B: p	q	p	q
W015i	6.06	5.94	5.5	4.28

Figure 18. Seedling stripe rust reaction to (A) single isolate W009 and (B) W015, grouped by two-locus genotypes at interacting loci *QYr.usw-5B* and *QYr.usw-7B*. There was a significant interaction between QTLs *QYr.usw-5B* and *QYr.usw-7B* ($P < 0.01$). 'p' represented the allele from Kofa, while 'q' represented the allele from W9262-260D3.

6 Discussion

6.1 Association mapping

6.1.1 Genetic diversity and population structure

Population structure and kinship matrices are used in AM studies to reveal the genetic structure of populations because population structure can cause spurious correlations between phenotypic and genotypic data (Patterson, et al., 2006; McVean, 2009; Hoffman, 2013). In this study, the sub-population assignment has coincidence with their geographic origin (Figure 7), which is consistent with the way of collecting the accessions in the AM panel representing genetic and geographic diversity of durum cultivars. Cultivars from Canada, the US and Mexico tended to cluster as a specific single sub-population, which indicated little admixture among these geographic locations. European and South American cultivars grouped into three or more sub-populations, which indicated that germplasm exchange had occurred. For the 92 accessions in the AM population, 79% were assigned explicitly to a specific sub-population, with population membership coefficient (Q value) greater than 80%. The other 19 accessions were assigned ambiguously with Q value less than 80% but greater than 40%, which also indicated low level of sub-population admixture (Appendices 7 and 8).

According to the Bayesian clustering model implemented by STRUCTURE and Structure Harvester, the association-mapping panel could be divided into three or five genetically distinguishable groups. Because both three and five major clusters could be identified in the phylogenetic tree and clustering of the AM population into either three or five groups was consistent with their geographic origin (Figure 7), it was not possible to differentiate between three or five sub-populations. However, results of association analyses using three and five sub-populations identified an identical region on chromosome 7BL associated with stripe rust resistance. These results suggest that both Q matrices adequately adjusted for population structure.

A Q-Q plot is a useful visual tool to check for deviation of observed *P*-values from the expected null hypothesis. True associations could deviate from the expected null hypothesis at the tail end of the distribution. Inflated *P*-value distributions can be caused by undetected genome deletions/duplications or uncorrected kinship and

population structure (de Bakker, et al., 2008). Deflation of *P*-values can be caused by phenotypic data discord or over-correction of inflation factors (kinships and population structure) (Schork, et al., 2013; Sternberg, 2014). In this study, the models without systematic inflation or deflation were chosen trait by trait, e.g., MLM_K=3 and MLM_K=5 for MI, MLM_K=3 and MLM_K=5 for single isolate W009, GLM_K=5, MLM_K=3 and MLM_K=5 for single isolate W015, and MLM_K=3, MLM_K=5 for field data Trans_AUDPC_Mexico2013. All the MLMs, which included both population structure and kinship matrix, were fit in the association analysis, no matter if the AM panel was assigned into three or five sub-populations (Figure 11).

The genome-wide distribution of SNP markers was used to explore genetic variation in the durum wheat population. The average polymorphism information content (PIC) values of the SNP markers was 0.292. Compared to previous association mapping studies of durum wheat, the 63 landraces from the Mediterranean basin had an average PIC value of 0.70 for SSR markers (Moragues, et al., 2007). Reimer (2008) indicated that the average PIC values for SSR markers were 0.40, essentially the same as the AM population used in the present study. A relatively low PIC values for SNP markers are expected because of their bi-allelic nature; the maximum PIC value is 0.5 when two alleles have identical frequency, while SSR markers do not have such a limitations (Amar, et al., 2011). Chao et al., (2009) indicated that the average PIC value of SNP markers was about three times lower than SSR markers based on the same population, and SNPs have less power to detect population structure (Amar, et al., 2011). However, despite this disadvantage, SNP markers are more abundant across the genome (Wang, et al., 2014), and SNPs are preferable for whole-genome association studies because their high throughput and automation of the analysis (Zhu, et al., 2008). In this study, the average density of SNP markers was 1.13 SNPs / cM. With SSR markers in other studies the average number of markers ranged from 70 (Maccaferri, et al., 2005) to 554 markers (Mantovani, et al., 2008), with a density of 0.099 to 0.270 markers / cM (Maccaferri, et al., 2008).

In this study, SNPs with minor allele frequency < 10% were removed before association analysis, because such markers cannot have large linkage disequilibrium

compared with markers with identical allele frequency, even if the makers were in complete linkage disequilibrium (Scherer, 2014). Therefore, markers with low MAF (e.g., 5%) have significantly more false positives than markers with higher MAF (e.g. 25%~50%) (Tabangin, et al., 2009). Moreover, low MAF markers are less informative and have less power to detect associations (Tabangin, et al., 2009). As a result, many GWAS removed SNPs with MAFs < 5% (Daly, et al., 2001; Plenge, et al., 2007; Abdurakhmonov, et al., 2008) or 10% (Cupples, et al., 2007; Florez, et al., 2007).

Instead of taking an arbitrary value (normally 0.10 or 0.20) as the LD threshold adopted in previous studies (Remington, et al., 2001; Nordborg, et al., 2002; Palaisa, et al., 2003), the 95% quantile r^2 values of unlinked SNP markers was used in the AM population as the critical r^2 value. The 95% quantile r^2 value was a population-specific threshold value, which can reflect the population structure of the AM population (Breseghello and Sorrells, 2006). At this significant threshold ($r^2 \geq 0.129$), the genome-wide average LD decayed rapidly after 5.9 cM (Figure 5). Previous studies have indicated that the estimated LD of durum wheat ranges from 2-3 (Somers, et al., 2007) to 20 cM ($r^2 \geq 0.2$) (Maccaferri, et al., 2005).

6.1.2 Phenotypic expression of stripe rust resistance

The ANOVA of the phenotypic data (Tables 10 and 11) confirmed that accessions had a significant effect ($P < 0.05$) on seedling stripe rust resistance, whereas the random effect of replication was non-significant. Therefore, the population was well suited to the AM study because the resistance level was highly variable among accessions, and the phenotypic data were consistent across replications.

The seedling disease reaction of MI, and single isolates W009 and W015 were highly correlated ($P < 0.001$), but some lines in the AM panel were susceptible to one isolate but not the other, e.g., Canadian cultivar DH696 and CDC Verona were resistant to W009 with an IT of 3.39 and 3.61, respectively, but susceptible to W015 with ITs of 6.13 and 5.74, which indicates the isolates are likely different from each other. Indeed the QTL identified on 7BL was similar for both isolates, suggesting that one or more genes in this interval protect against both isolates.

For the field experiments, Mexico2013 was transformed to normality to minimize variation, Leth2012_AM and Leth2013_AM were not normally distributed even after square-root transformation attempts, because of the high proportion of resistant accessions (Figures 3A and B). To calculate AUDPC for seedling resistance or adult plant resistance, at least three rating points should be collected at identical time intervals. However, in the seedling resistance experiments, the first rating was made when the average disease severity of the susceptible check (Avocet) reached IT 7, the second rating was made two days later. The third rating was not possible because the infected leaves died shortly after the second rating.

Comparisons between seedling and adult plant reaction indicated that some accessions (Zone 1 of Table 26) were resistant at the adult plant stage, while susceptible at the seedling stage. Some accessions were consistently resistant or susceptible at both adult plant and seedling stages (Zone 2 and Zone 3 of Table 26). The different disease reactions of Zone 1 accessions suggested that APR genes played a role after plants passed the seedling stage and became mature. Combining seedling and adult plant resistance genes in breeding programs may be the best strategy to protect plants from severe infection at the seedling stage, and to avoid rapid resistance breakdown.

Table 26. Seedling and adult plant reactions for a selection of accessions from the AM population. Seedling reactions with IT ≥ 4 and adult plant reaction with severity ≥ 20% are indicated in red.

Zone	Accession	Origin	MI	W009	W015	Leth2013	03sep2013_Mexico
	Buck Topacio	Argentina	5.7	4.2	5.4	5.0	5.0
	DT705	Canada	5.1	3.6	4.2	5.0	1.7
	DT707	Canada	4.3	4.2	4.3	5.0	0.0
	Duilio	Italy	6.9	5.7	4.3	5.0	3.3
1	Simeto	Italy	7.5	6.0	4.7	5.0	1.7
	Svevo	Italy	8.2	7.3	5.5	5.0	1.7
	Green 34	Mexico	6.5	6.4	4.3	5.0	5.0
	Nacori 97	Mexico	6.3	4.1	4.7	5.0	0.0
	Borli	Spain	7.7	7.2	4.7	5.0	0.0
	Buck Ambar	Argentina	1.7	1.8	2.1	5.0	0.0
	Carioca	France	1.8	1.6	2.2	5.0	3.3
	Durabon	Germany	3.5	2.4	3.2	5.0	3.3
	D-73-15	Iran	2.4	2.6	2.9	5.0	1.7
	Arcobaleno	Italy	2.3	2.2	2.1	5.0	0.0
	Ciccio	Italy	3.8	3.0	3.6	8.3	3.3
	Grazia	Italy	2.7	2.7	4.0	5.0	6.7
	Iride	Italy	2.7	2.1	2.1	5.0	0.0
2	Parsifal	Italy	2.0	2.1	2.1	5.0	8.3
	Tresor	Italy	2.3	2.8	3.2	8.3	0.0
	DHTON 1	Morocco	3.2	2.7	3.2	5.0	3.3
	Arrivato	New Zealand	1.8	1.6	2.2	5.0	0.0
	CFR5001	New Zealand	2.8	2.4	2.7	5.0	3.3
	CRDW17	New Zealand	1.9	2.0	3.2	5.0	3.3
	Altar-Aos	Spain	3.9	2.7	2.3	5.0	1.7
	Gallareta	Spain	1.8	2.2	2.1	5.0	5.0
	Bon. Quilaco	Argentina	8.1	7.1	7.0	31.7	50.0
	920334	Australia	8.1	6.7	5.9	51.7	46.7
	940030	Australia	8.3	7.1	6.7	25.0	63.3
	AC Morse	Canada	8.3	7.1	6.8	8.3	46.7
	AC Navigator	Canada	8.8	7.6	7.3	21.7	50.0
	AC Pathfinder	Canada	8.9	7.6	6.1	71.7	70. 0
	Commander	Canada	7.5	6.6	6.8	18.3	33.3
	DT536	Canada	8.9	7.3	6.9	15.0	33.3
	DT709	Canada	8.0	6.8	6.1	11.7	43.3
3	Agridur	France	8.8	7.3	6.5	61.7	76.7
	Durafit	Germany	8.3	7.3	6.8	25.0	33.3
	Bronte	Italy	7.8	6.4	6.1	25.0	46.7
	K-39099	Russia	8.1	7.1	6.5	13.3	43.3
	Kofa	U.S.	8.3	6.9	5.7	31.7	23.3
	Ocotillo	U.S.	8.4	7.3	6.4	28.3	43.3
	Westbred881	U.S.	8.7	7.2	6.9	65.0	80.0
	Strongfield	Canada	6.4	4.5	5.2	51.7	18.3
	Varano	Italy	7.9	6.4	5.3	38.3	21.7
$LSD_{0.05}$	/	/	0.8	0.7	0.6	10.8	4.1

When the AM panel was divided into five sub-populations, the second sub-population was more resistant in several independent experiments, e.g., seedling resistance to MI, single isolates W009 and W015, and adult plant resistance in Mexico 2013 and Lethbridge 2012 and 2013. The origin of accessions in the second sub-population (Table 15) was Spain, Italy, Argentina, France, New Zealand, Iran and Australia. These accessions have potential as sources of resistance in the development of cultivars adapted to the Canadian Prairies.

6.2 Identification of QTL for Stripe Rust Resistance

Transgressive segregation was observed for seedling resistance and adult plant resistance to stripe rust in the DH population (Figures 14A and C), which may indicate the complementary action of genes from two parents (Rick and Smith, 1953). This was observed as Mendelian, and QTL analysis confirmed that each gene produced a protein that contributed to resistance on its own, but when the two genes were expressed together, two proteins acted together to produce a more resistant phenotype. The DH population of the cross Kofa x W9262-260D3 was screened with single isolates W009 and W015 under controlled conditions. According to the parental reaction, IT 4 was chosen to differentiate resistance and susceptibility. The 155 lines in the DH population segregated as 113 susceptible and 31 resistant to W009, and 112 susceptible and 32 resistant to W015, which fitted well to a 3:1 ratio. It suggested that two unlinked genes for resistance existed in the DH population. The quantitative genetic analysis confirmed two unlinked major QTLs located on chromosomes 5BL and 7BL. One quarter of the DH lines were resistant and contained these two QTLs. The genetic variance explained 55.7% of the phenotypic variance for seedling resistance to W009 and 52.8% to W015. Transgressive segregation was reported in many other rust resistance studies in hexaploid wheat (Krupinsky and Sharp, 1979; Zhang, et al., 2001; Wallwork and Johnson, 1984; Jacobs and Broers, 1989; Milus and Line, 1986). Wallwork and Johnson (1984) observed increased resistance or susceptibility to single isolates of stripe rust compared to either parents in progenies from F1 to F5; Zhang et al., (2001) observed transgressive segregation in resistant by resistant crosses and Milus and Line (1986) also observed transgressive segregation in wheat for HTAP.

The bi-parental mapping population was screened using the same single isolates as was used in the AM panel, therefore, we can therefore make a comparison between the QTL(s) identified by AM and the genetic mapping method. The QTL located on chromosome 7BL need further research, because significant markers were detected on chromosome 7BL in four independent experiments (seedling resistance to MI, single isolates W009 and W015, and adult plant resistance AUDPC_Mexico2013). These significant loci were further confirmed by QTL detection in the bi-parental mapping population.

Through QTL mapping, *QYr.usw-7B* was detected on chromosome 7BL with flanking markers at 2.9 cM and 4.1 cM away using single isolates W009 and W015. Through AM, the major QTL was located at the most distal end of chromosome 7BL, within a 1.5 cM interval flanked by the SNP markers Tdurum_contig61884_836 and Excalibur_c51720_84. Therefore, the genetic resolution of *QYr.usw-7B* detected in QLT mapping was further improved by AM.

The QTL *QYr.usw-5B*, was seedling resistance gene located on chromosome 5B, seedling resistance genes *Yr19* and *Yr47* were previously identified to be located on the same chromosome (Appendix 1). They were not contained in the differential sets (Appendix 11), and no significant SSR markers ($P < 0.05$) were associated with *QYr.usw-5B*, which makes the comparison between *QYr.usw-5B* and either *Yr19* or *Yr47* impossible.

Comparison of *QYr.usw-7B* with other *Yr* genes located on chromosome 7B, *Yr2*, *Yr6*, *Yr39, Yr52, Yr59, Yr67, YrZH84* and *YrMY37*. The genes *Yr39, Yr52* and *Yr59* were excluded from consideration because they were HTAP genes and were unlikely to function at the seedling stage. Seedling resistance gene *Yr2* was not effective against W009 and W015 (Table 27). Seedling resistance gene *Yr6* was excluded because it is located on chromosome 7BS (Macer, 1963; Labrum, 1980; El-Bedewy and Robbelen, 1982; Chen, et al., 1995). Recessive seedling resistance gene *YrMY37* was also likely excluded because it is located on chromosome 7BL close to the centromere instead of telomeric region (Ren, et al., 2015).

Table 27. The avirulence/virulence formulas of single isolates W009 and W015.

Pathotype	Avirulence / Virulence Formula
W009	**Yr** 1,3a,3b,4a,4b,5,10,15,18,24,26,36,SP,Su,Tye / **Yr** A,2,6,7,8,9,17,18,25,27,28,29,31,VII
W015	**Yr** 1,3b,4b,5,15,18,36,SP,Su,Tye / **Yr** A,2,3a,4a,6,7,8,9,10,17,18,24,25,26,27,28,29,31,32,CV,VII

The *Yr67* gene (previously named *YrC591*) and *YrZH84* were mapped in the telomeric region of chromosome 7BL of wheat (Figure 19, Appendix 12). Li, et al. (2006) identified a major seedling resistance gene on chromosome 7BL in Chinese winter wheat Zhou 8425B, designated *YrZH84*. Li, et al. (2009) identified a major seedling resistance gene on chromosome 7BL in cultivar C591, designated *YrC591*, and it was officially named *Yr67*. *YrZH84* and *YrC591* were flanked by Xcfa2040-7B and Xbarc182 with genetic distance of 1.4 cM and 8.4 cM, and 2.8 cM and 0.4 cM, respectively (Li, et al., 2006; Ren, et al., 2012) (Figure 19). When seed of Zhou 8425B (*YrZH84*) and C591 (*Yr67*) become available, further comparative allelic studies can be made.

Although further studies need to be done to compare the location of *Yr67* and *YrZH84* with *QYr.usw-7B*, most known stripe rust resistance genes show dominant inheritance, except three recessive inherited genes, *YrSph*, *YrLM168* and *YrMY37*, have been located on chromosome 2AS, 6A and 7BL close to the centromere region, respectively (Ren, et al., 2015). Thus recessive inherited gene *QYr.usw-7B* is likely a new recessive stripe rust resistance identified in durum.

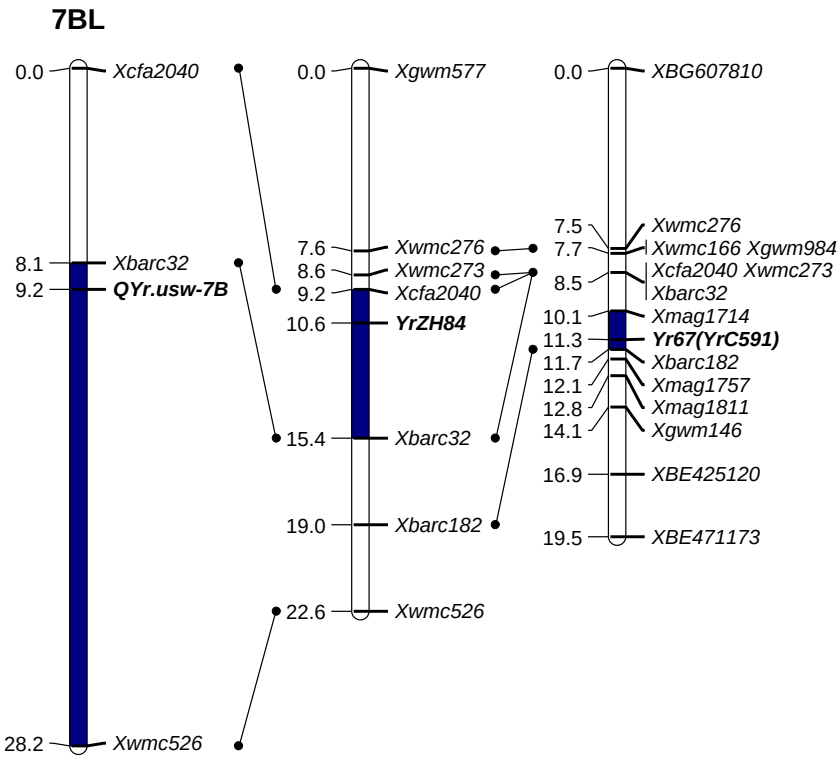


Figure 19. Positions of previously reported *Yr* genes (in bold) on chromosome 7BL of durum wheat. Genetic distance in cM is indicated on the left.

Information of the virulence spectrum of plant pathogens is crucial knowledge for breeding programs. Virulence studies are currently being conducted at the University of Saskatchewan. Thirty-two differential wheat genotypes are used, including 21 NILs, 10 supplemental wheat lines and 1 triticale line (Appendix 11). The 21 near-isogenic lines (NILs) have Avocet-*YrA* as the recurrent parent. Avocet-*YrA* (WW119/WW15//Egret) was a reselected line from the Australian *Triticum aestivum* 'Avocet', which carried the leaf rust resistance genes *Lr10* and *Lr13* and none of the known *Yr* resistance genes (Navabi, et al., 2005). The avirulence / virulence formula for these two pathogens provided Table 27 (Appendix 4). The differentiation between avirulence and virulence was chosen as IT 4. Isolate W009 was less virulent than W015, because W009 was virulent on less *Yr* genes, although both were virulent on *Yr2* and *Yr6*.

Analysis of the haplotype-trait association analysis is helpful for precise location of preferred alleles for breeding (Barrero, et al., 2011). For the haplotype of markers associated with seedling and adult plant resistance, 15 closely linked markers form one haplotype block of five major haplotypes (Table 19). Using the popular Canadian cultivar Strongfield as a genetic check, the nucleotide diversity of other cultivars of durum was determined in Appendix 10. The haplotype of Strongfield was almost the same as the resistant accessions, which have seedling disease severity score (IT) < 4, but the LS mean of the seedling reaction (IT) of Strongfield against MI was actually 6.42. This indicated that the genetic background of the QTL is also critical for resistance expression, e.g. *Yr3* was not effective against stripe rust in Vilmorin backgrounds, while highly resistant in a Nord Desprez background (Raza, 2012). Therefore, selection decisions in breeding programs to combat stripe rust must be made according to both the phenotyping and MAS.

7 Conclusions and future work

Genetic studies to identify and map stripe rust (*Puccinia striiformis* f.sp. *tritici*) resistance genes in durum wheat were conducted only recently (Bansal, et al., 2014; Cheng, et al., 2014; Chen, 2014). Stripe rust was not considered an economically important disease on the western prairies of Canada before 2000. However, after the epidemic of stripe rust in southern Alberta and Saskatchewan in 2010 and 2011, stripe rust resistance has become an important objective of durum breeding programs in Saskatchewan. Therefore, it is important to identify potential stripe rust resistance genes in durum germplasm.

Screening the AM panel allowed us to: i. characterize stripe rust resistant lines in elite durum germplasm, and ii. detect genetic variation for stripe rust resistance in the AM panel to identify major loci associated with seedling and adult plant resistance. In this study, two QTLs were identified using QTL mapping, *QYr.usw-5B* and *QYr.usw-7B.* The major locus detected using AM was located on chromosome 7BL, which was the same region as *QYr.usw-7B*. Thus, this locus was observed with high frequency and was widespread in different genetic backgrounds of the AM panel. The QTL *QYr.usw-5B* had a smaller effect could not be detected in the AM panel, because it was almost fixed in cultivated lines. We can further screen the germplasm using molecular markers associated with *QYr.usw-7B* and *QYr.usw-5B* to determine if most of the breeding lines carry the genetic region linked to these two major QTLs. Identifying other effective resistance genes is also important. Because the protection of major QTL is not guaranteed in the future, it is risky to rely on a single major QTL to maintain the stipe rust resistance in the breeding program. Therefore, combining other effective resistance genes via MAS is an important and sound strategy. The availability of SNP platforms for wheat greatly facilitates marker-assisted selection at chromosome 7BL and other target regions (Akhunov, et al., 2009).

Several mapping projects in hexaploid wheat have identified for other disease resistance genes, e.g., stem rust, leaf rust and powdery mildew, located on chromosome 7BL (Nematollahi, et al., 2008; Crossa, et al., 2007). Further studies can be made to determine whether accessions in the AM panel contain these three genes, so that co-inheritance of powdery mildew and rust resistance genes may be possible in

the breeding program. For the accessions that contain multiple resistance genes, fine mapping of the distal region of chromosome 7BL should be conducted.

Finally, sequencing and cloning *QYr.usw-7B* could provide further information on this important genetic region, e.g., the physiology of plant-pathogen interaction and exploitation for genetic engineering (Maccaferri, et al., 2010; Qiu, et al., 2009). A number of disease resistance genes have been cloned from wheat, including *Lr10*, *Lr21* (leaf rust resistance genes) and *Pm3* (powdery mildew resistance gene) (Keller, et al., 2005; Keller, et al., 2007). Sequencing of *QYr.usw-7B* can provide further evidence to verify its similarity to *Yr67* and *YrZH84*.

8 Reference

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Appendix 1. Chromosomal locations, original germplasm sources and references of genes for resistance to stripe rust [*Puccinia striiformis* f. sp. *tritici*].

***Yr* gene**	**Chr.**	**Original Source**	**Resistance type[a]**	**Reference**
Yr1	2AL	Chinese 166	RS, AS	(Lupton and Macer, 1962)
Yr2	7B	Heines Vll	RS, AS	(Lupton and Macer, 1962)
Yr3a	1B	Capelle Desprez	RS, AS	(Lupton and Macer, 1962)
Yr3b	1B	Hybrid 46	RS, AS	(Lupton and Macer, 1962)
Yr3c	1B	Minister	RS, AS	(Lupton and Macer, 1962)
Yr4a	6B	Capelle Desprez	RS, AS	(Lupton and Macer, 1962)
Yr4b	6B	Hybrid 46	RS, AS	(Lupton and Macer, 1962)
Yr5	2BL	*T. spelta* Album	RS, AS	(Macer, 1963)
Yr6	7BS	Heines Kolben	RS, AS	(Macer, 1963)
Yr7	2BL	Lee	RS, AS	(Macer, 1963)
Yr8	2DL	Compair	RS, AS	(Riley, et al., 1968)
Yr9	1RS/1BL	Clement	RS, AS	(Macer, 1975)
Yr10	1BS	Moro	RS, AS	(Macer, 1975)
Yr11	NA	Joss Chambier	AP	(Priestley, 1978)
Yr12	NA	Frontier	AP	(Priestley, 1978)
Yr13	NA	Hustler	AP	(Priestley, 1978)
Yr14	NA	Kador	AP	(Priestley, 1978)
Yr15	1BS	*T. dicoccoides* G-25	RS, AS	(Gerechter-Amitai, et al., 1989)
Yr16	2DS	Bersee	NRS, AP	(Worland and Law, 1986)
Yr17	2AS	VPM1	RS, AS	(Bariana and McIntosh, 1994)
Yr18	7DS	Jupateco 73R	NRS, HTAP	(Ma and Singh, 1996)
Yr19	5B	Compair	RS, AS	(Chen, et al., 1995)
Yr20	6D	Fielder	RS, AS	(Chen, et al., 1995)
Yr21	1B	Lemhi	RS, AS	(Chen, et al., 1995)
Yr22	4D	Lee	RS, AS	(Chen, et al., 1995)
Yr23	6D	Lee	RS, AS	(Chen, et al., 1995)
Yr24	1BS	Yr24/6*AVS	RS, AS	(McIntosh and Lagudah, 2000)
Yr25	1D	Strubes Dickkopf	RS, AS	(Calonnec and Johnson, 1998)
Yr26	1BS	R55	RS, AS	(Yildirim, et al., 2000)
Yr27	2BS	Ciano 79	RS, AS	(McDonald, et al., 2004)
Yr28	4DS	Synthetic	RS, AS	(Singh, et al., 2000)
Yr29	1BL	Pavon F76	NRS, AP	(Singh, et al., 2005)
Yr30	3BS	Opata 85	NRS, AP	(Singh, et al., 2005)
Yr31	2BS	Pastor	RS, AS	(McIntosh, et al., 2003)

Yr32	2AS	Carstens V	RS, AS	(Eriksen, et al., 2004)
Yr33	7DL	Batavia	RS, AS	(Zahravi, et al., 2003)
Yr34	5AL	WAWHT2046	AP	(Bariana, et al., 2006)
Yr35	6BS	98M71	RS, AS	(Marais, et al., 2005a)
Yr36	6BS	Glupro, RSL No.65	NRS, HTAP	(Uauy, et al., 2005)
Yr37	2DL	S14	RS, AS	(Marais, et al., 2005b)
Yr38	6AS	Line 03524	RS, AS	(Marais, et al., 2006)
Yr39	7BL	Alpowa	NRS, HTAP	(Lin and Chen, 2007)
Yr40	5DS	T5DL.5DS.5MgS	RS, AS	(Kuraparthy, et al., 2007)
Yr41	2BS	Chuannong19	RS, AS	(Luo, et al., 2005; 2006)
Yr42	6AL/6AS	03M119-71A	RS, AS	(Marais, et al., 2009)
Yr43	2BL	IDO377s	RS, AS	(Cheng and Chen, 2010)
Yr44	2BL	Zak	RS, AS	(Sui, et al., 2009)
Yr45	3DL	PI 181434	RS, AS	(Li, et al., 2011)
Yr46	4DL	RL 6077	NRS, AP	(Herrera-Foessel, et al., 2011)
Yr47	5BS	AUS 28183	RS, AS	(Bansal, et al., 2011)
Yr48	5AL	PI 610750	RS, AS	(Lowe, et al., 2011)
Yr49	3DS	Chuanmai 18	RS, AP	(Spielmeyer et al., unpublished)
Yr50	4BL	TAI 7047	RS, AS	(Liu, et al., 2013)
Yr51	4AL	AUS 91456	RS, AS	(Randhawa, et al., 2014)
Yr52	7BL	PI 183527	NRS, HTAP	(Ren, et al., 2012)
Yr53	2BL	Durum PI 480148	RS, AS	(Xu, et al., 2013)
Yr54	2DL	Quaiu 3	NRS, AP	(Basnet, et al., 2014)
Yr55	2DL	NA	NA	(Bariana, 2013 Personal communication)
Yr56	2AS	NA	NA	(Bariana, 2013 Personal communication)
Yr57	3BS	NA	NA	(Bariana, 2013 Personal communication)
Yr58	3BL	NA	NA	(Bansal. 2013 Personal communication)
Yr59	7BL	PI 178759	NRS, HTAP	(Zhou, et al., 2014)
Yr60	4AL	NA	NA	(Herrera-Foessel, et al., 2013)
Yr61	7AS	Pindong 34	NRS, AP	(Hao, et al., 2011)
Yr62	4BL	PI 192252	NRS, HTAP	(Lu, et al., 2014)
Yr63	7BS	AUS 27955	NA	(Bansal and Bariana, 2013 Personal communication)
Yr64	1BS	Durum PI 331260	RS, AS	(Cheng, et al., 2014)
Yr65	1BS	Durum PI 480016	RS, AS	(Cheng, et al., 2014)
Yr66	3DS	NA	NA	(Bansal, 2014 Personal communication)
Yr67	7BL	C591	RS, AS	(Li, et al., 2009)

[a]AS, All-stage resistance (also called seedling resistance); AP, adult-plant resistance; HTAP, high-temperature, adult-plant resistance; RS, race-specific resistance; NRS, non-race-specific resistance.

Appendix 2. Origin and pedigree information for the association mapping population

Accession	Origin	Pedigree
Bonaerance Inta Cumenay	Argentina	Unknown
Bonaerance Quilaco	Argentina	MAGH72//GS/AA///RABI//D21563/AA
Bonaerance Valverde	Argentina	GIORGIO//CAPELLI/YUMA
Buck Ambar	Argentina	Unknown
Buck Topacio	Argentina	Unknown
920334	Australia	69850/ 86014
940030	Australia	Unknown
940435	Australia	Unknown
940955	Australia	Unknown
950329	Australia	Unknown
950844	Australia	Unknown
Tamaroi	Australia	RUFF/FLAMINGO-DW//MEXICALI-75///SHEARWATER/56113/TAM-1-B-17/KAMILAROI/56112/WELLS/56111//GUILLEMOT
Wollaroi	Australia	TAM-1-B-17/(SIB)KAMILAROI//ROKEL(S)/(SIB)KAMILAROI
9661-AF1D	Canada	W9262-260D3/ARUBA//DT 662
9661-CA5E	Canada	W9262-260D3/ARUBA//DT 662
AC Avonlea	Canada	8267-AD2A/DT 61
AC Melita	Canada	MEDORA/LLOYD
AC Morse	Canada	RL 7196/DT 610
AC Napoleon	Canada	VIC/DT384//DT 471
AC Navigator	Canada	KYLE/WESTBRED881
AC Pathfinder	Canada	WESTBRED 881/DT 367
Commander	Canada	W9260-BK03/AC NAVIGATOR//AC PATHFINDER
D24-1773	Canada	DT 520/D94078

DT513	Canada	DT 625/DT 612
DT536	Canada	D94350/D93108
DT540	Canada	D95253/D95116
DT691	Canada	DT618/ 8667-D216C//DT 637
DT695	Canada	DT 471/2*KYLE
DT696	Canada	DT618/DT 637//KYLE
DT704	Canada	AC AVONLEA/DT 665
DT705	Canada	AC AVONLEA/DT 665
DT707	Canada	AC AVONLEA/DT 665
DT709	Canada	DT 674/DT 665
DT710	Canada	DT618/Green 27
DT711	Canada	Westbred 881/W9260-BK03
Kyle	Canada	6962-92-8-5/ 6965-494-
Strongfield	Canada	AC Avonlea/DT 665
Agridur	France	EDMORE//CIMMYT 303/CHANDUR
Ariesol	France	Unknown
Carioca	France	CID 479402
RABD 93.40	France	Unknown
Tetradur	France	EDMORE//CAPDUR/REGAL
Durabon	Germany	SIGNADUR/EDM//P 4312.86
Durafit	Germany	Unknown
44616	Iran	Unknown
44721	Iran	Unknown
D-73-15	Iran	Unknown
Arcobaleno	Italy	CHEN/ALTAR 84
Bronte	Italy	BERILLO/LATINO
Ciccio	Italy	APPULO/VALNOVA//VALFORTE/PATRIZIO

Colosseo	Italy	CRESO/MEXA
Demetra	Italy	MESSAPIA/GIOIA
Duilio	Italy	CAPPELLI//ANHINGA/FLAMINGO
Fortore	Italy	CAPEITI 8/VALFORTE
Gianni	Italy	Unknown
Grazia	Italy	ISWRN-21/VALSELVA
Iride	Italy	ALTAR 84/ARES-SIB
Lesina	Italy	Unknown
Mongibello	Italy	TRINAKRIA/VALFORTE
Nedda	Italy	TRINAKRIA/VALFORTE
Parsifal	Italy	INRA92-1/D81028
Simeto	Italy	CAPEITI/VALNOVA
Svevo	Italy	SELEZIONE CIMMYT/ZENIT-SIB
Tresor	Italy	AMBER-DURUM/S-22-80
Varano	Italy	CAPEITI 8/CRESO//CRESO///VALFORTE/TRINAKRIA
Green 27	Mexico	STERNA-DW 2/GRAVELOTE
Green 34	Mexico	STERNA-DW 2/GRAVELOTE
Nacori 97	Mexico	ALTAR 84/CMH82A.1062//CD58230-?
Vitron	Mexico	TURCHIA-77///JORI-SIB/ANHINGA-SIB//FLAMINGO-SIB
DHTON 1	Morocco	Unknown
Gidara 17a	Morocco	Unknown
Marjak	Morocco	Unknown
Arrivato	New Zealand	Unknown
CFR5001	New Zealand	Unknown
CRDW17	New Zealand	Unknown
K-39099	Russia	LV-URAZOVSKII R-N,VORONEZHSKAYA OBL
Altar-Aos	Spain	Unknown

Borli	Spain	Unknown
Camacho	Spain	Unknown
Gallareta	Spain	RUFF/FLAMINGO-DW//MEXICALI-75/3/SHEARWATER/4/?
Mexa	Spain	GDOVZ469///JO 1//61.130/LDS
D940027	U.S.	D88104/D88207
D940098	U.S.	D88450/D87436
D941038	U.S.	D86117/D88289
D95580	U.S.	BELZER/D88058//D88276
Durex	U.S.	AZ-MFSRS-86
Kofa	U.S.	DICOCCUM ALPHA
Kronos	U.S.	APB MSFRS POP SEL (D03-21)
Langdon	U.S.	LDN240/KHAPLI//LANGDON 308///MINDUM*3/VERNAL/4/VERNAL EMMER/3*MINDUM
Ocotillo	U.S.	Unknown
Plaza	U.S.	PLENTY/D8291
Westbred881	U.S.	WARD/WLS//CNDO/WCA///MEXI/WB1000

Appendix 3. List of core microsatellite markers used for population structure determination.

Marker	Chromosome	Distance (cM)
wmc818	1A	29
cfa2219	1A	124
barc8	1B	25
wmc44	1B	92
wmc407	2A	15
cfd168	2A	85
wmc154	2B	29
wmc332	2B	93
wmc532	3A	6
wmc594	3A	105
gwm389	3B	1
wmc632	3B	143
wmc491	4A	8
wmc219	4A	88
wmc47	4B	10
wmc710	4B	48
gwm443	5A	23
gwm291	5A	163
wmc740	5B	56
gwm497	5B	164
gwm334	6A	2
wmc254	6A	148
wmc487	6B	9
barc24	6B	55
wmc283	7A	40
cfa2040	7A	119
gwm537	7B	41
wmc311	7B	118

Appendix 4. Least square means (LSM) and summary of seedling stripe rust reaction to single isolates W009 and W015 (infection type: 0-9) within the differential sets evaluated in the phytotron at the University of Saskatchewan.

Differential sets	Yr Gene Present	*Puccinia striiformis* f. sp. *Tritici* isolates	
		W009	W015
07YR02	*YrA*	7.5	6.6
07YR03	*Yr1*	0.9	1.1
07YR04	*Yr2*	6.3	6.5
07YR05	*Yr5*	1.0	0.9
07YR06	*Yr6*	7.9	6.3
07YR07	*Yr7*	7.5	5.9
07YR08	*Yr8*	5.6	5.1
07YR09	*Yr9*	7.2	6.1
07YR10	*Yr10*	1.8	4.9
07YR11	*Yr15*	0.3	0.5
07YR12	*Yr17*	7.1	6.5
07YR13	*Yr18*	7.7	6.3
07YR14	*Yr24*	2.5	4.5
07YR15	*Yr26*	2.4	4.4
07YR16	*Yr27*	6.3	5.6
07YR17	*YrSP*	1.6	1.9
07YR18	*YrCV* or *Yr32*	3.8	4.0
07YR19	*Yr28*	6.9	6.3
07YR20	*Yr29*	7.6	6.5
07YR21	*Yr31*	7.0	6.3
AC Avonlea	Unknown	6.8	5.5
AC Barrie	Unknown	6.4	6.1
CDC Teal	Unknown	6.7	5.4
Chinese 166	*Yr1*	1.0	1.1
Heines 7	*Yr2, YrVII, Yr25*	5.1	4.6
Hybrid 46	*Yr3b, Yr4b*	1.4	1.9
Lillian	*Yr18, Yr36*	3.0	3.8
Nord Deprez	*Yr3a, Yr4a*	3.1	4.1
Suwan 92* Omar	*YrSu*	2.5	3.2
Tyee	*YrTye*	0.9	1.0
Susceptible checks			
07YR01 (S)	Null	7.2	7.5
Brevis (S)	Unknown	5.0	4.4

Appendix 5. Least square means (LSM) and summary of seedling stripe rust reaction to MI, single isolates W009 and W015 (infection type: 0-9) within the association mapping population evaluated in the phytotron at the University of Saskatchewan.

Accession	MI		W009		W015	
	Scoring_1	Scoring_2	Scoring_1	Scoring_2	Scoring_1	Scoring_2
Bonaerance Inta Cumenay	5.1	5.7	2.6	3.4	4.5	4.6
Bonaerance Quilaco	7.5	8.1	6.4	7.1	6.9	7.0
Bonaerance Valverde	6.0	7.3	5.6	7.2	3.9	5.3
Buck Ambar	1.6	1.7	1.8	1.8	2.1	2.1
Buck Topacio	3.5	5.7	3.4	4.2	4.9	5.4
920334	6.5	8.1	5.4	6.7	5.4	5.9
940030	8.4	8.3	6.3	7.1	6.6	6.7
940435	4.5	6.3	5.1	6.9	3.9	4.2
940955	6.3	7.9	5.2	6.7	4.0	4.4
950329	6.6	8.1	6.0	7.7	4.9	5.6
950844	7.4	8.4	6.9	7.0	5.1	5.7
Tamaroi	4.7	6.0	4.5	4.7	3.9	4.1
Wollaroi	4.4	6.9	3.7	5.0	3.2	3.7
9661-AF1D	6.3	7.2	5.0	5.9	5.1	5.2
9661-CA5E	5.1	6.3	4.2	4.3	3.4	3.6
AC Avonlea	4.7	5.0	4.0	4.5	3.7	3.9
AC Melita	6.4	7.9	5.4	6.1	4.0	4.5
AC Morse	7.4	8.3	6.2	7.1	6.6	6.8
AC Napoleon	4.4	4.3	2.2	2.2	4.2	4.7
AC Navigator	7.6	8.8	7.7	7.6	6.6	7.3
AC Pathfinder	7.8	8.9	6.5	7.6	5.8	6.1
Commander	5.4	7.5	6.1	6.6	6.4	6.8
D24-1773	4.5	5.9	4.1	5.3	4.0	4.6
DT513	5.5	6.9	3.4	4.6	3.6	4.2
DT536	6.7	8.9	6.9	7.3	6.9	6.9
DT540	3.6	5.2	3.1	3.6	4.7	5.7

DT691	5.4	5.9	3.4	3.3	4.4	4.2
DT695	5.9	5.8	2.6	2.5	3.9	3.9
DT696	4.4	5.8	2.7	3.4	5.7	6.1
DT704	7.2	8.2	6.2	7.0	6.3	6.5
DT705	4.4	5.1	3.1	3.6	3.4	4.2
DT707	4.2	4.3	4.3	4.2	3.8	4.3
DT709	7.2	8.0	5.9	6.8	5.5	6.1
DT710	5.6	6.5	3.8	4.3	3.6	3.9
DT711	7.1	7.6	5.6	6.5	5.2	6.3
Kyle	4.4	5.4	3.7	4.7	3.7	4.8
Strongfield	4.6	6.4	4.0	4.5	4.5	5.2
Agridur	8.4	8.8	7.3	7.3	6.7	6.5
Ariesol	5.1	6.3	4.5	4.5	4.0	4.5
Carioca	2.0	1.8	1.8	1.6	1.8	2.2
RABD 93.40	4.0	5.3	3.1	4.3	2.9	3.1
Tetradur	3.6	4.8	3.1	3.7	3.2	3.0
Durabon	3.8	3.5	2.5	2.4	3.0	3.2
Durafit	7.1	8.3	7.0	7.3	6.0	6.8
44616	4.9	6.4	4.0	4.1	3.3	3.5
44721	5.2	6.9	5.3	6.3	3.1	3.7
D-73-15	2.7	2.4	2.4	2.6	2.7	2.9
Arcobaleno	2.1	2.3	2.1	2.2	2.0	2.1
Bronte	7.0	7.8	6.0	6.4	5.8	6.1
Ciccio	3.2	3.8	2.7	3.0	3.3	3.6
Colosseo	4.7	6.3	5.1	6.0	5.2	5.5
Demetra	3.6	5.8	6.0	6.8	5.0	5.1
Duilio	5.8	6.9	4.1	5.7	4.1	4.3
Fortore	3.6	6.7	3.4	3.7	2.8	3.3
Gianni	7.8	7.9	6.4	6.9	5.7	5.8
Grazia	2.4	2.7	2.6	2.7	3.7	4.0
Iride	2.5	2.7	2.3	2.1	2.0	2.1

Lesina	5.0	7.7	4.4	5.5	3.9	4.5
Mongibello	6.3	7.3	5.1	6.3	4.9	5.3
Nedda	4.9	7.5	3.4	4.8	4.1	5.0
Parsifal	1.9	2.0	2.1	2.1	2.1	2.1
Simeto	5.0	7.5	4.0	6.0	4.4	4.7
Svevo	8.0	8.2	6.4	7.3	5.4	5.5
Tresor	1.5	2.3	2.5	2.8	2.8	3.2
Varano	6.2	7.9	5.6	6.4	4.9	5.3
Green 27	5.9	7.9	6.6	7.4	4.0	4.6
Green 34	5.1	6.5	5.2	6.4	4.1	4.3
Nacori 97	4.2	6.3	3.1	4.1	3.6	4.7
Vitron	7.4	8.8	6.7	6.7	4.8	4.8
DHTON 1	3.1	3.2	2.5	2.7	2.9	3.2
Gidara 17a	5.7	7.9	6.8	7.7	4.1	4.9
Marjak	4.0	5.0	2.8	3.5	2.5	2.4
Arrivato	1.8	1.8	1.4	1.6	2.0	2.2
CFR5001	2.0	2.8	2.4	2.4	2.4	2.7
CRDW17	2.3	1.9	1.8	2.0	3.1	3.2
K-39099	7.3	8.1	7.1	7.1	6.3	6.5
Altar-Aos	3.2	3.9	2.4	2.7	2.2	2.3
Borli	6.3	7.7	6.1	7.2	4.7	4.7
Camacho	4.5	5.3	2.3	2.7	3.1	3.2
Gallareta	1.8	1.8	2.1	2.2	1.9	2.1
Mexa	5.0	6.9	6.0	6.7	4.2	5.3
D940027	5.5	7.5	5.8	7.0	5.2	5.6
D940098	3.5	4.7	4.0	4.6	3.9	4.6
D941038	4.6	6.0	3.7	3.7	4.6	5.0
D95580	3.8	4.7	2.7	2.7	3.9	4.2
Durex	4.2	5.4	2.9	3.0	2.6	2.6
Kofa	7.8	8.3	6.7	6.9	5.4	5.7
Kronos	6.3	7.7	4.5	5.7	3.2	3.2

Langdon Dic 6B	6.8	7.7	4.7	6.5	3.1	3.4
Ocotillo	7.5	8.4	7.0	7.3	5.8	6.4
Plaza	4.1	3.1	2.5	2.5	5.1	5.0
Westbred881	8.1	8.7	7.1	7.2	6.7	6.9
Mean (pop.)	5.1	6.1	4.4	5.0	4.2	4.6
Min (pop.)	1.5	1.7	1.4	1.6	1.8	2.1
Max (pop.)	8.4	8.9	7.7	7.7	6.9	7.3
Average LSD 0.05	0.8	0.8	0.7	0.7	0.6	0.6

Appendix 6. Least square means (LSM) and summary of adult plant resistance (disease severity in percentile) within the association mapping population evaluated in Lethbridge 2012, 2013 and Mexico 2013.

Accession	Leth2012_AM	Leth2013_AM	19aug2013_Mexico	27aug2013_Mexico	03sep2013_Mexico	AUDPC_Mexico2013
Bonaerance Inta Cumenay	15.0	5.0	8.3	11.7	11.7	161.7
Bonaerance Quilaco	15.0	31.7	33.3	36.7	50.0	583.3
Bonaerance Valverde	15.0	21.7	20.0	18.3	20.0	287.5
Buck Ambar	15.0	5.0	0.0	0.0	0.0	0.0
Buck Topacio	25.0	5.0	6.7	5.0	5.0	81.7
920334.0	20.0	51.7	30.0	40.0	46.7	583.3
940030.0	80.0	25.0	26.7	43.3	63.3	653.3
940435.0	15.0	28.3	13.3	18.3	26.7	284.2
940955.0	75.0	18.3	15.0	21.7	23.3	304.2
950329.0	15.0	18.3	10.0	18.3	20.0	247.5
950844.0	15.0	5.0	10.0	11.7	13.3	174.2
Tamaroi	25.0	5.0	6.7	10.0	10.0	136.7
Wollaroi	15.0	5.0	5.0	6.7	8.3	99.2
9661-AF1D	30.0	18.3	11.7	11.7	11.7	175.0
9661-CA5E	15.0	5.0	3.3	1.7	1.7	31.7
AC Avonlea	45.0	5.0	10.0	10.0	8.3	144.2
AC Melita	15.0	38.3	20.0	23.3	26.7	348.3
AC Morse	20.0	8.3	40.0	43.3	46.7	648.3
AC Napoleon	50.0	15.0	16.7	13.3	13.3	213.3
AC Navigator	45.0	21.7	36.7	40.0	50.0	621.7
AC Pathfinder	20.0	71.7	43.3	56.7	70.0	843.3
Commander	50.0	18.3	23.3	26.7	33.3	410.0
D24-1773	70.0	41.7	13.3	11.7	13.3	187.5
DT513	30.0	5.0	8.3	8.3	8.3	125.0
DT536	45.0	15.0	23.3	33.3	33.3	460.0

DT540	10.0	5.0	10.0	8.3	8.3	131.7
DT691	75.0	11.7	23.3	30.0	33.3	435.0
DT695	35.0	51.7	33.3	43.3	50.0	633.3
DT696	10.0	5.0	10.0	16.7	20.0	235.0
DT704	40.0	5.0	23.3	30.0	30.0	423.3
DT705	35.0	5.0	1.7	1.7	1.7	25.0
DT707	75.0	5.0	3.3	0.0	0.0	13.3
DT709	25.0	11.7	26.7	36.7	43.3	533.3
DT710	60.0	21.7	6.7	6.7	6.7	100.0
DT711	45.0	18.3	13.3	15.0	15.0	218.3
Kyle	35.0	11.7	16.7	15.0	15.0	231.7
Strongfield	50.0	51.7	16.7	16.7	18.3	255.8
Agridur	85.0	61.7	40.0	56.7	76.7	853.3
Ariesol	10.0	5.0	13.3	13.3	13.3	200.0
Carioca	25.0	5.0	3.3	3.3	3.3	50.0
RABD 93.40	45.0	8.3	11.7	11.7	11.7	175.0
Tetradur	15.0	11.7	11.7	11.7	11.7	175.0
Durabon	20.0	5.0	5.0	3.3	3.3	56.7
Durafit	15.0	25.0	26.7	33.3	33.3	473.3
44616.0	60.0	18.3	10.0	8.3	10.0	137.5
44721.0	25.0	5.0	6.7	5.0	6.7	87.5
D-73-15	25.0	5.0	1.7	1.7	1.7	25.0
Arcobaleno	15.0	5.0	1.7	0.0	0.0	6.7
Bronte	45.0	25.0	23.3	33.3	46.7	506.7
Ciccio	25.0	8.3	3.3	3.3	3.3	50.0
Colosseo	25.0	5.0	11.7	15.0	20.0	229.2
Demetra	15.0	5.0	10.0	10.0	11.7	155.8
Duilio	25.0	5.0	5.0	3.3	3.3	56.7
Fortore	30.0	15.0	6.7	8.3	8.3	118.3
Gianni	15.0	18.3	13.3	13.3	15.0	205.8
Grazia	10.0	5.0	6.7	6.7	6.7	100.0

Iride	45.0	5.0	0.0	0.0	0.0	0.0
Lesina	30.0	15.0	10.0	10.0	10.0	150.0
Mongibello	15.0	5.0	10.0	10.0	11.7	155.8
Nedda	20.0	5.0	8.3	11.7	13.3	167.5
Parsifal	25.0	5.0	8.3	8.3	8.3	125.0
Simeto	40.0	5.0	1.7	1.7	1.7	25.0
Svevo	30.0	5.0	1.7	1.7	1.7	25.0
Tresor	30.0	8.3	0.0	0.0	0.0	0.0
Varano	15.0	38.3	13.3	16.7	21.7	254.2
Green 27	10.0	5.0	11.7	15.0	16.7	217.5
Green 34	15.0	5.0	3.3	3.3	5.0	55.8
Nacori 97	15.0	5.0	0.0	0.0	0.0	0.0
Vitron	15.0	8.3	15.0	20.0	26.7	303.3
DHTON 1	15.0	5.0	3.3	3.3	3.3	50.0
Gidara 17a	15.0	5.0	13.3	15.0	16.7	224.2
Marjak	15.0	8.3	6.7	8.3	8.3	118.3
Arrivato	15.0	5.0	3.3	0.0	0.0	13.3
CFR5001	10.0	5.0	3.3	3.3	3.3	50.0
CRDW17	20.0	5.0	5.0	3.3	3.3	56.7
K-39099	25.0	13.3	33.3	36.7	43.3	560.0
Altar-Aos	10.0	5.0	1.7	1.7	1.7	25.0
Borli	30.0	5.0	1.7	1.7	0.0	19.2
Camacho	10.0	5.0	1.7	0.0	0.0	6.7
Gallareta	15.0	5.0	5.0	5.0	5.0	75.0
Mexa	15.0	8.3	11.7	10.0	15.0	174.2
D940027	15.0	25.0	18.3	23.3	23.3	330.0
D940098	75.0	15.0	8.3	6.7	6.7	106.7
D941038	60.0	15.0	10.0	13.3	15.0	192.5
D95580	45.0	5.0	5.0	3.3	3.3	56.7
Durex	15.0	5.0	11.7	11.7	13.3	180.8
Kofa	45.0	31.7	16.7	20.0	23.3	298.3

Kronos	25.0	21.7	10.0	11.7	11.7	168.3
Langdon Dic 6B	65.0	25.0	20.0	23.3	30.0	360.0
Ocotillo	30.0	28.3	28.3	36.7	43.3	540.0
Plaza	15.0	5.0	15.0	13.3	13.3	206.7
Westbred881	75.0	65.0	43.3	56.7	80.0	878.3
Mean (pop.)	30.1	14.8	13.0	15.1	17.6	226.9
Min (pop.)	10.0	5.0	0.0	0.0	0.0	0.0
Max (pop.)	85.0	71.7	43.3	56.7	80.0	878.3
Average LSD 0.05	/	10.8	3.7	3.8	4.1	51.2

Appendix 7. Q matrix as assigned by STRUCTURE for K = 5 sub-populations based on 20 independent runs using 28 unlinked SSR markers. Population membership coefficients greater than 0.800 were indicated in bold.

		Population					
Accession	Origin	1	2	3	4	5	Population Assignment K=5
920334	Australia	**0.965**	0.007	0.004	0.017	0.007	1
940030	Australia	**0.993**	0.001	0.003	0.002	0.001	1
940435	Australia	**0.993**	0.002	0.002	0.002	0.001	1
940955	Australia	**0.994**	0.002	0.002	0.001	0.001	1
950329	Australia	0.729	0.002	0.005	0.259	0.005	1
950844	Australia	**0.942**	0.008	0.008	0.036	0.006	1
Wollaroi	Australia	**0.937**	0.003	0.049	0.003	0.008	1
Buck Ambar	Argentina	0.009	0.762	0.004	0.123	0.101	2
Buck Topacio	Argentina	0.116	0.410	0.212	0.012	0.250	2
Tamaroi	Australia	0.014	**0.956**	0.005	0.023	0.002	2
Carioca	France	0.010	0.743	0.005	0.051	0.192	2
44616	Iran	0.003	**0.897**	0.015	0.034	0.051	2
Colosseo	Italy	0.031	0.658	0.002	0.007	0.301	2
Iride	Italy	0.002	**0.992**	0.002	0.003	0.002	2
Arcobaleno	Italy	0.001	**0.992**	0.002	0.003	0.002	2
Gidara 17a	Morocco	0.030	0.518	0.005	0.149	0.298	2
CFR5001	New Zealand	0.002	**0.993**	0.002	0.002	0.001	2
Altar-Aos	Spain	0.001	**0.992**	0.001	0.003	0.002	2
Borli	Spain	0.003	**0.963**	0.002	0.025	0.007	2
Gallareta	Spain	0.002	**0.993**	0.002	0.002	0.002	2
9661-AF1D	Canada	0.003	0.006	**0.844**	0.003	0.143	3

9661-CA5E	Canada	0.004	0.002	**0.988**	0.003	0.004	3
AC Avonlea	Canada	0.002	0.001	**0.994**	0.001	0.001	3
AC Melita	Canada	0.003	0.003	**0.978**	0.013	0.003	3
AC Morse	Canada	0.003	0.006	**0.987**	0.003	0.002	3
AC Napoleon	Canada	0.002	0.002	**0.992**	0.003	0.002	3
AC Navigator	Canada	0.002	0.002	**0.991**	0.002	0.003	3
AC Pathfinder	Canada	0.002	0.001	**0.994**	0.002	0.002	3
Commander	Canada	0.002	0.002	**0.992**	0.002	0.003	3
D24-1773	Canada	0.009	0.006	**0.979**	0.003	0.002	3
DT513	Canada	0.002	0.001	**0.995**	0.001	0.001	3
DT536	Canada	0.004	0.002	**0.811**	0.177	0.005	3
DT540	Canada	0.001	0.002	**0.991**	0.003	0.002	3
DT691	Canada	0.003	0.001	**0.993**	0.002	0.001	3
DT695	Canada	0.184	0.002	**0.809**	0.002	0.002	3
DT696	Canada	0.008	0.003	**0.942**	0.026	0.021	3
DT704	Canada	0.002	0.004	**0.990**	0.003	0.001	3
DT705	Canada	0.002	0.003	**0.991**	0.003	0.001	3
DT707	Canada	0.001	0.001	**0.995**	0.001	0.002	3
DT709	Canada	0.002	0.004	**0.990**	0.003	0.002	3
DT711	Canada	0.003	0.002	**0.992**	0.002	0.002	3
Kyle	Canada	0.002	0.002	**0.992**	0.002	0.002	3
Strongfield	Canada	0.002	0.002	**0.993**	0.002	0.001	3
Tetradur	France	0.060	0.005	0.497	0.040	0.398	3
Durabon	Germany	0.004	0.004	**0.955**	0.031	0.006	3
Durafit	Germany	0.002	0.001	**0.992**	0.002	0.003	3
D940027	U.S.	0.042	0.009	0.737	0.015	0.197	3
D941038	U.S.	0.007	0.003	0.657	0.329	0.003	3

D95580	U.S.	0.012	0.002	**0.980**	0.003	0.004	3
Durex	U.S.	0.003	0.105	**0.818**	0.007	0.067	3
Kofa	U.S.	0.002	0.003	**0.982**	0.002	0.011	3
Langdon Dic 6B	U.S.	0.360	0.003	0.626	0.005	0.005	3
Ocotillo	U.S.	0.003	0.002	**0.987**	0.003	0.005	3
Plaza	U.S.	0.011	0.013	**0.973**	0.002	0.001	3
Westbred881	U.S.	0.002	0.004	**0.970**	0.003	0.021	3
Bonaerance Quilaco	Argentina	0.004	0.002	0.115	**0.873**	0.005	4
DT710	Canada	0.010	0.004	0.074	**0.905**	0.007	4
Ariesol	France	0.003	0.006	0.421	0.567	0.003	4
44721	Iran	0.004	0.115	0.018	0.684	0.179	4
D-73-15	Iran	0.017	0.062	0.218	0.552	0.151	4
Bronte	Italy	0.005	0.013	0.004	**0.864**	0.114	4
Duilio	Italy	0.001	0.003	0.002	**0.993**	0.001	4
Gianni	Italy	0.002	0.003	0.002	**0.993**	0.002	4
Parsifal	Italy	0.018	0.004	0.005	**0.952**	0.020	4
Simeto	Italy	0.001	0.003	0.002	**0.992**	0.001	4
Svevo	Italy	0.003	0.002	0.004	**0.988**	0.003	4
Green 27	Mexico	0.009	0.008	0.006	**0.969**	0.007	4
Green 34	Mexico	0.005	0.003	0.003	**0.988**	0.002	4
Nacori 97	Mexico	0.006	0.160	0.004	**0.823**	0.007	4
Vitron	Mexico	0.002	0.005	0.002	**0.990**	0.001	4
DHTON 1	Morocco	0.004	0.015	0.005	**0.964**	0.012	4
Arrivato	New Zealand	0.003	0.024	0.004	**0.959**	0.011	4
K-39099	Russia	0.007	0.005	0.003	**0.983**	0.002	4
Mexa	Spain	0.005	0.061	0.016	0.738	0.179	4
Kronos	U.S.	0.002	0.004	0.035	**0.951**	0.007	4

Bonaerance Inta Cumenay	Argentina	0.002	0.008	0.001	0.003	**0.986**	5
Bonaerance Valverde	Argentina	0.003	0.004	0.164	0.003	**0.826**	5
RABD 93.40	France	0.006	0.002	0.012	0.005	**0.976**	5
Agridur	France	0.003	0.091	0.258	0.010	0.638	5
Ciccio	Italy	0.002	0.002	0.002	0.002	**0.992**	5
Demetra	Italy	0.004	0.006	0.002	0.010	**0.978**	5
Fortore	Italy	0.005	0.005	0.003	0.002	**0.985**	5
Grazia	Italy	0.064	0.002	0.068	0.010	**0.855**	5
Lesina	Italy	0.002	0.002	0.003	0.002	**0.991**	5
Nedda	Italy	0.002	0.004	0.003	0.003	**0.988**	5
Mongibello	Italy	0.001	0.004	0.007	0.002	**0.985**	5
Tresor	Italy	0.006	0.007	0.217	0.015	0.755	5
Varano	Italy	0.002	0.002	0.002	0.002	**0.993**	5
Marjak	Morocco	0.003	0.002	0.002	0.392	0.600	5
CRDW17	New Zealand	0.217	0.150	0.003	0.053	0.577	5
Camacho	Spain	0.004	0.002	0.006	0.004	**0.984**	5
D940098	U.S.	0.007	0.131	0.268	0.136	0.459	5

Appendix 8. Q matrix as assigned by STRUCTURE for K = 3 sub-populations based on 20 independent runs using 28 unlinked SSR markers. Population membership coefficients greater than 0.800 were indicated in bold.

Accession	Origin	Population			Population Assignment K=3
		1	2	3	
Bonaerance Quilaco	Argentina	0.698	0.007	0.295	1
Buck Ambar	Argentina	0.573	0.421	0.006	1
Buck Topacio	Argentina	**0.848**	0.039	0.114	1
920334	Australia	0.722	0.012	0.266	1
950329	Australia	**0.923**	0.010	0.067	1
950844	Australia	**0.971**	0.006	0.023	1
Tamaroi	Australia	**0.989**	0.004	0.007	1
DT710	Canada	0.691	0.030	0.279	1
Ariesol	France	0.535	0.005	0.460	1
Carioca	France	**0.980**	0.016	0.004	1
44721	Iran	**0.938**	0.040	0.022	1
D-73-15	Iran	0.595	0.139	0.266	1
Arcobaleno	Italy	**0.993**	0.004	0.004	1
Bronte	Italy	0.711	0.282	0.006	1
Duilio	Italy	**0.994**	0.002	0.003	1
Gianni	Italy	**0.994**	0.002	0.003	1
Iride	Italy	**0.992**	0.005	0.003	1
Parsifal	Italy	**0.975**	0.011	0.014	1
Simeto	Italy	**0.994**	0.003	0.003	1
Svevo	Italy	**0.969**	0.013	0.018	1
Green 27	Mexico	**0.965**	0.017	0.018	1

Green 34	Mexico	**0.988**	0.003	0.008	1
Nacori 97	Mexico	**0.974**	0.020	0.007	1
Vitron	Mexico	**0.995**	0.002	0.003	1
DHTON 1	Morocco	**0.983**	0.011	0.005	1
Arrivato	New Zealand	**0.966**	0.029	0.004	1
CFR5001	New Zealand	**0.992**	0.004	0.003	1
K-39099	Russia	**0.980**	0.009	0.011	1
Altar-Aos	Spain	**0.992**	0.005	0.003	1
Borli	Spain	**0.991**	0.006	0.003	1
Gallareta	Spain	**0.990**	0.005	0.005	1
Mexa	Spain	**0.941**	0.042	0.017	1
Kronos	U.S.	**0.904**	0.013	0.083	1
Bonaerance Inta Cumenay	Argentina	0.007	**0.991**	0.002	2
Bonaerance Valverde	Argentina	0.007	0.753	0.240	2
RABD 93.40	France	0.017	**0.923**	0.060	2
44616	Iran	0.165	0.795	0.040	2
Ciccio	Italy	0.004	**0.991**	0.005	2
Colosseo	Italy	0.142	**0.853**	0.005	2
Demetra	Italy	0.007	**0.989**	0.004	2
Fortore	Italy	0.005	**0.988**	0.007	2
Grazia	Italy	0.043	0.668	0.289	2
Lesina	Italy	0.004	**0.988**	0.008	2
Mongibello	Italy	0.004	**0.984**	0.012	2
Nedda	Italy	0.004	**0.992**	0.005	2
Tresor	Italy	0.027	0.654	0.318	2
Varano	Italy	0.004	**0.992**	0.004	2

Gidara 17a	Morocco	0.468	0.526	0.006	2
Marjak	Morocco	0.247	0.746	0.006	2
CRDW17	New Zealand	0.333	0.660	0.007	2
Camacho	Spain	0.005	**0.981**	0.014	2
940030	Australia	0.398	0.004	0.597	3
940435	Australia	0.375	0.003	0.621	3
940955	Australia	0.392	0.004	0.604	3
Wollaroi	Australia	0.007	0.039	**0.955**	3
9661-AF1D	Canada	0.009	0.191	**0.800**	3
9661-CA5E	Canada	0.004	0.005	**0.991**	3
AC Avonlea	Canada	0.002	0.002	**0.996**	3
AC Melita	Canada	0.018	0.005	**0.977**	3
AC Morse	Canada	0.009	0.003	**0.988**	3
AC Napoleon	Canada	0.005	0.003	**0.992**	3
AC Navigator	Canada	0.005	0.007	**0.989**	3
AC Pathfinder	Canada	0.003	0.003	**0.994**	3
Commander	Canada	0.004	0.005	**0.992**	3
D24-1773	Canada	0.006	0.009	**0.985**	3
DT513	Canada	0.002	0.002	**0.995**	3
DT536	Canada	0.167	0.008	**0.825**	3
DT540	Canada	0.005	0.003	**0.991**	3
DT691	Canada	0.003	0.002	**0.995**	3
DT695	Canada	0.007	0.003	**0.989**	3
DT696	Canada	0.008	0.019	**0.973**	3
DT704	Canada	0.008	0.002	**0.990**	3
DT705	Canada	0.007	0.003	**0.990**	3

DT707	Canada	0.002	0.003	**0.995**	3
DT709	Canada	0.009	0.004	**0.988**	3
DT711	Canada	0.004	0.003	**0.993**	3
Kyle	Canada	0.004	0.004	**0.991**	3
Strongfield	Canada	0.004	0.002	**0.993**	3
Agridur	France	0.094	0.363	0.543	3
Tetradur	France	0.087	0.376	0.537	3
Durabon	Germany	0.040	0.011	**0.949**	3
Durafit	Germany	0.004	0.005	**0.991**	3
D940027	U.S.	0.050	0.154	0.796	3
D940098	U.S.	0.396	0.167	0.436	3
D941038	U.S.	0.135	0.009	**0.856**	3
D95580	U.S.	0.004	0.006	**0.989**	3
Durex	U.S.	0.124	0.104	0.772	3
Kofa	U.S.	0.004	0.021	**0.975**	3
Langdon Dic 6B	U.S.	0.011	0.006	**0.983**	3
Ocotillo	U.S.	0.006	0.008	**0.986**	3
Plaza	U.S.	0.009	0.002	**0.988**	3
Westbred881	U.S.	0.008	0.022	**0.970**	3

Appendix 9. Population assignment as indicated by STRUCTURE for K = 3 and K = 5 sub-populations based on 20 independent runs using 28 unlinked SSR markers.

Accession	Origin	Population Assignment K=3	Population Assignment K=5
Bonaerance Quilaco	Argentina	1	4
Buck Ambar	Argentina	1	2
Buck Topacio	Argentina	1	2
920334	Australia	1	1
950329	Australia	1	1
950844	Australia	1	1
Tamaroi	Australia	1	2
DT710	Canada	1	4
Ariesol	France	1	4
Carioca	France	1	2
44721	Iran	1	4
D-73-15	Iran	1	4
Arcobaleno	Italy	1	2
Bronte	Italy	1	4
Duilio	Italy	1	4
Gianni	Italy	1	4
Iride	Italy	1	2
Parsifal	Italy	1	4
Simeto	Italy	1	4
Svevo	Italy	1	4
Green 27	Mexico	1	4
Green 34	Mexico	1	4
Nacori 97	Mexico	1	4
Vitron	Mexico	1	4
DHTON 1	Morocco	1	4
Arrivato	New Zealand	1	4
CFR5001	New Zealand	1	2
K-39099	Russia	1	4
Altar-Aos	Spain	1	2
Borli	Spain	1	2
Gallareta	Spain	1	2
Mexa	Spain	1	4
Kronos	U.S.	1	4
Bonaerance Inta Cumenay	Argentina	2	5
Bonaerance Valverde	Argentina	2	5
RABD 93.40	France	2	5
44616	Iran	2	2
Ciccio	Italy	2	5
Colosseo	Italy	2	2
Demetra	Italy	2	5

Fortore	Italy	2	5
Grazia	Italy	2	5
Lesina	Italy	2	5
Mongibello	Italy	2	5
Nedda	Italy	2	5
Tresor	Italy	2	5
Varano	Italy	2	5
Gidara 17a	Morocco	2	2
Marjak	Morocco	2	5
CRDW17	New Zealand	2	5
Camacho	Spain	2	5
940030	Australia	3	1
940435	Australia	3	1
940955	Australia	3	1
Wollaroi	Australia	3	1
9661-AF1D	Canada	3	3
9661-CA5E	Canada	3	3
AC Avonlea	Canada	3	3
AC Melita	Canada	3	3
AC Morse	Canada	3	3
AC Napoleon	Canada	3	3
AC Navigator	Canada	3	3
AC Pathfinder	Canada	3	3
Commander	Canada	3	3
D24-1773	Canada	3	3
DT513	Canada	3	3
DT536	Canada	3	3
DT540	Canada	3	3
DT691	Canada	3	3
DT695	Canada	3	3
DT696	Canada	3	3
DT704	Canada	3	3
DT705	Canada	3	3
DT707	Canada	3	3
DT709	Canada	3	3
DT711	Canada	3	3
Kyle	Canada	3	3
Strongfield	Canada	3	3
Agridur	France	3	5
Tetradur	France	3	3
Durabon	Germany	3	3
Durafit	Germany	3	3
D940027	U.S.	3	3
D940098	U.S.	3	5
D941038	U.S.	3	3
D95580	U.S.	3	3

Durex	U.S.	3	3
Kofa	U.S.	3	3
Langdon Dic 6B	U.S.	3	3
Ocotillo	U.S.	3	3
Plaza	U.S.	3	3
Westbred881	U.S.	3	3

Appendix 10. Haplotype of stripe rust resistance QTL for the AM panel. The 92 accessions were sorted by the second rating of stripe rust reaction to MI, statistical analysis revealed highly significant association (permutation $P < 0.05$) between specific haplotype of 15 SNPs and disease severity. This table showed highly variable region of QTL located on chromosome 7BL. Canadian cultivar Strongfield was set as genetic check, and the haplotype that is same as Strongfield were highlighted by red.

Accessions	Scoring_2_MI	BobWhite_c12355_1590 / Tdurum_contig49575_1207	Excalibur_c1070_2327 / Kukri_c46447_1738	RAC875_rep_c111788_253	BS00022162_51	Kukri_c3781_285	Tdurum_contig42586_990	Excalibur_c51720_84	Kukri_c48418_149	RAC875_c54854_164	Tdurum_contig42586_290	Tdurum_contig42586_720	Tdurum_contig61884_836	Tdurum_contig49575_1237
Buck Ambar	1.67	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
Arrivato	1.75	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
Carioca	1.75	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Gallareta	1.83	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
CRDW17	1.90	AG	AG	AG	AG	AA	AA	AC	CC	AA	CC	GG	GG	AA
Parsifal	2.00	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
Arcobaleno	2.28	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Tresor	2.33	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
D-73-15	2.38	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Iride	2.67	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Grazia	2.72	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
CFR5001	2.75	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Plaza	3.12	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
DHTON 1	3.15	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Durabon	3.53	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Ciccio	3.75	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
Altar-Aos	3.92	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
DT707	4.25	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG

AC Napoleon	4.33	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
D940098	4.65	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
D95580	4.71	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Tetradur	4.84	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
AC Avonlea	4.96	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Marjak	5.02	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
DT705	5.08	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
DT540	5.17	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
RABD 93.40	5.25	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
Camacho	5.28	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
Durex	5.39	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Kyle	5.39	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Buck Topacio	5.71	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Bonaerance Inta Cumenay	5.71	AG	AG	AG	AG	AA	AA	AC	CC	AA	CC	GG	GG	AA
Demetra	5.75	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
DT696	5.75	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
DT695	5.78	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
DT691	5.89	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
D24-1773	5.92	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
D941038	6.03	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Tamaroi	6.04	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Colosseo	6.25	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
Nacori 97	6.29	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
940435	6.33	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
9661-Ca5E	6.33	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Ariesol	6.34	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
44616	6.40	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
Strongfield	6.42	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Green 34	6.50	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
DT710	6.54	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Fortore	6.72	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA

DT513	6.86	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Wollaroi	6.89	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Mexa	6.89	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
44721	6.92	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Duilio	6.92	AG	AG	AG	AG	AA	AA	AC	CC	AA	CC	GG	GG	AA
9661-AF1D	7.15	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
Bonaerance Valverde	7.25	AG	AG	AG	AG	AA	AA	AC	CC	AA	CC	GG	GG	AA
Mongibello	7.25	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Simeto	7.50	AG	AG	AG	AG	AA	AA	AC	CC	AA	CC	GG	GG	AA
Commander	7.50	AA	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
D940027	7.53	AG	AG	AA	AG	AA	AA	AC	CC	AG	CC	GG	AA	AA
Nedda	7.54	AG	AG	AG	AG	AA	AA	AC	CC	--	CC	GG	GG	AA
DT711	7.58	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Kronos	7.69	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Lesina	7.71	AG	AG	AG	AG	AA	AA	AC	CC	AA	CC	GG	GG	AA
Langdon Dic 6B	7.71	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Borli	7.72	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
Bronte	7.83	AG	AG	AG	AG	AA	AA	AC	AA	--	CC	GG	GG	AA
Varano	7.86	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
940955	7.86	AA	AA	AA	GG	GG	GG	CC	AC	AG	AA	AA	AA	AG
AC Melita	7.89	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Green 27	7.92	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
Gianni	7.92	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
Gidara 17a	7.94	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
DT709	8.00	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
920334	8.08	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
K-39099	8.08	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Bonaerance Quilaco	8.08	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
950329	8.13	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA

Svevo	8.17	AA	AA	AG	GG	GG	GG	CC	AC	AA	AA	AA	GG	AG
DT704	8.19	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
AC Morse	8.25	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Kofa	8.25	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Durafit	8.29	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG
940030	8.33	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Ocotillo	8.39	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
950844	8.42	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
Westbred881	8.72	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Vitron	8.75	AG	AG	AG	AG	AA	AA	AC	AA	AG	CC	GG	GG	AA
AC Navigator	8.75	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
Agridur	8.83	AA	AA	--	GG	AA	--	CC	CC	AA	--	--	--	AA
DT536	8.92	AG	AG	AG	AG	AA	AA	AC	CC	AG	CC	GG	GG	AA
AC Pathfinder	8.92	AA	AA	AA	GG	GG	GG	CC	AC	AA	AA	AA	AA	AG

Appendix 11. List of wheat differentials used in this study.

No.	Differential Lines	Pedigree	Yr Gene Present
1	07YR01	Avocet-*YrA*	Null
2	07YR02	Avocet+*YrA*	*YrA*
3	07YR03	YR1/6*AOC	*Yr1*
4	07YR04	Siete Cerros T66 (*Yr2*)	*Yr2*
5	07YR05	YR5/6*AOC	*Yr5*
6	07YR06	YR6/6*AOC	*Yr6*
7	07YR07	YR7/6*AOC	*Yr7*
8	07YR08	YR8/6*AOC	*Yr8*
9	07YR09	YR9/6*AOC	*Yr9*
10	07YR10	YR10/6*AOC	*Yr10*
11	07YR11	YR15/6*AOC	*Yr15*
12	07YR12	YR17/6*AOC	*Yr17*
13	07YR13	YR18/3*AOC	*Yr18*
14	07YR14	YR24/3*AOC	*Yr24*
15	07YR15	YR26/3*AOC	*Yr26*
16	07YR16	YR27/6*AOC	*Yr27*
17	07YR17	YRSP/6*AOC	*YrSP*
18	07YR18	YRCV/6*AOC	*YrCV* or *Yr32*
19	07YR19	Yr28	*Yr28*
20	07YR20	Yr29	*Yr29*
21	07YR21	Yr31	*Yr31*
22	AC Avonlea	AC Avonlea	Unknown
23	AC Barrie	AC Barrie	Unknown
24	Brevis (Triticale)	Triticale	Unknown
25	CDC Teal	CDC Teal	Unknown
26	Chinese 166	Chinese 166	*Yr1*
27	Heines 7	Heines 7	*Yr2, YrVII, Yr25*
28	Hybrid 46	Hybrid 46	*Yr3b, Yr4b*
29	Lillian	Lillian	*Yr18, Yr36*
30	Nord Deprez	Nord Deprez	*Yr3a, Yr4a*
31	Suwan 92* Omar	Suwan 92* Omar	*YrSu*
32	Tyee	Tyee	*YrTye*

Appendix 12. Summary of QTL located on chromosome 7B associated with stripe rust resistance (Rosewarne, et al., 2013).

Chromosome region	Source	Markers	References
QRYr7B.1	Oligoculm	*Xgwm935.3* *Xgwm46*	(Suenaga, et al., 2003)
QRYr7B.1	Stephens	*wPt-7653* *Xwmc76*	(Vazquez, et al., 2012)
QRYr7B.1	SHA3/CBRD	*Xbarc176* *wPt-8106, wPt-9467*	(Ren, et al., 2012)
QRYr7B.2	Alpowa	*Xggp36* *Xgwm131, Xgwm43*	(Lin and Chen, 2007)
QRYr7B.2	Kukri	*wPt-3723* *wPt-8921*	(Bariana, et al., 2010)
QRYr7B.3	Attila	*Xgwm344*	(Rosewarne, et al., 2008)
QRYr7B.3	Pastor	*wPt-3190* *(Xgwm577, Xpsr680b)*	(Rosewarne, et al., 2012)
QRYr7B.3	SHA3/CBRD	*Xgwm577* *wPt-4300, wPt-5309*	(Ren, et al., 2012)
YrZH84	Zhou 8425B	*Xcfa2040-7B,* *Xbarc32-7B*	(Li, et al., 2006)
YrC591 (*Yr67*)	C591	*Xcfa2040-7B*	(Li, et al., 2009)
YrMY37	Mianmai 37	*Xgwm297, Xbarc267*	(Ren, et al., 2015)